CALIFORNIA FISH and GAME

"CONSERVATION THROUGH EDUCATION"

VOLUME 82 FALL 1996 NUMBER 4

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CALIFORNIA FISH AND GAME

VOLUME 82 FALL 1996 NUMBER 4

Published Quarterly by

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COMPARATIVE FEEDING HABITS OF JUVENILE CHINOOK SALMON, STEELHEAD, AND SACRAMENTO SQUAWFISH IN THE LOWER AMERICAN RIVER, CALIFORNIA

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We compared diets of juvenile chinook salmon, *Oncorhynchus tshawytscha*, steelhead, *O. mykiss*, and Sacramento squawfish, *Ptychocheilus grandis*, in the lower American River from February through July 1992 and 1993. Chinook salmon and steelhead fed primarily on chironomids (all stages), baetids (adults and nymphs), and hydropsychids (larvae and pupae); their diets overlapped significantly in May and June. Squawfish diet consisted mainly of corixid adults and chironomid larvae and did not overlap significantly with either chinook salmon or steelhead diets. Food habits changed somewhat as the season progressed and the fish increased in size. In 1993, chinook salmon and steelhead fed less than in the previous year and relied more on chironomids. We attribute these differences in diet to the major fluctuations in discharge and lower water temperatures that occurred in the lower American River that year.

INTRODUCTION

The American River, a major tributary of the Sacramento River, is typical of most rivers in the United States in that it has experienced various perturbations such as impoundment, introduction of exotic fish species, and pollution (Allan and Flecker 1993). The only reach of the American River with unobstructed flow is the 39-km section in Sacramento County between Nimbus Dam and the confluence with the Sacramento River. Although flows are controlled by Nimbus and Folsom dams, the lower American River (LAR) still supports a varied fish community, including substantial spawning runs of chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *O. mykiss*, which are supplemented by fingerlings from Nimbus Fish Hatchery; hatchery-reared chinook fingerlings are trucked downstream to Carquinez Strait for release. The LAR provides critical nursery habitat for these salmonids from hatching in winter and spring to smoltification in late spring into fall.

Water development projects proposed for the LAR, such as extension of the Folsom South Canal and East Bay Municipal Utility District withdrawals, would alter or reduce flows. Understanding the impact of these projects requires thorough knowledge of the ecology of the river's fish assemblage, including trophic relationships.

---

[1] Present Address: East Bay Municipal Utility District, 108 C West Turner Road, Lodi, California 95240.

As a step in that direction, we conducted an analysis of the diets of juvenile chinook salmon and steelhead in the LAR. We also analyzed food habits of juvenile Sacramento squawfish, *Ptychocheilus grandis*, because it is another abundant predatory species in the LAR whose young frequently have been observed in the same habitats as chinook and steelhead (Brown et al.[2] 1992). Historically, this species has been considered a competitor with young salmonids (Pintler and Johnson 1958, Burns 1966, Brown and Moyle 1982). Our specific objectives were to compare diets and feeding patterns of juvenile chinook salmon, steelhead, and Sacramento squawfish on a monthly basis for 2 consecutive years during the months that all three species were present in the LAR.

STUDY AREA

The LAR is characterized by alternating bar complex and flatwater habitats, with a gradient of approximately 0.6 m per km. The drainage area consists of 179 km^2 of mostly urbanized land. Several small streams and storm drains enter the river. At least 28 fish species are found in the LAR (Snider and Titus[3] 1994). Among the most abundant species, in addition to chinook salmon, steelhead, and Sacramento squawfish, are the Sacramento sucker, *Catostomus occidentalis*; prickly sculpin, *Cottus asper*; and tule perch, *Hysterocarpus traski*. Other anadromous species found seasonally are the Pacific lamprey, *Lampetra tridentata*; American shad, *Alosa sapidissima*; and striped bass, *Morone saxatilis*.

Mean daily flows during the 1992 study period were relatively constant, approximately 25 m^3/s from February through May, then gradually increased to a maximum of 127 m^3/s in June (Fig. 1). In contrast, flows during the 1993 study period were higher and more variable; several major fluctuations involved abrupt changes in a short time. Highest flow that year was 430 m^3/s in early April followed by an abrupt drop to 30 m^3/s, the lowest flow since February.

Water temperatures gradually increased during the study period in both years, but temperatures were considerably higher in 1992, increasing from about 11°C in February to about 19°C in late June (Fig. 2). In 1993, temperatures averaged about 3°C lower than in 1992 throughout the study period.

METHODS

Fish were collected monthly between 1 February and 1 July 1992 and 1993 at three locations: 1) downstream from the H Street bridge (river km 10), 2) Gristmill (river km 17), and 3) above the Sunrise Boulevard bridge (river km 32). These sites

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[2] Brown, L., P. Moyle, and D. Vanicek. 1992. American River studies: Intensive fish surveys, March-June, 1991. Mimeo Report, Department of Wildlife and Fisheries Biology, University of California, Davis, California, USA.

[3] Snider, W. and R. Titus. 1994. Fish community survey, lower American River, January-July 1994. Mimeo Report, California Department of Fish and Game, Environmental Services Division, Sacramento, California, USA.

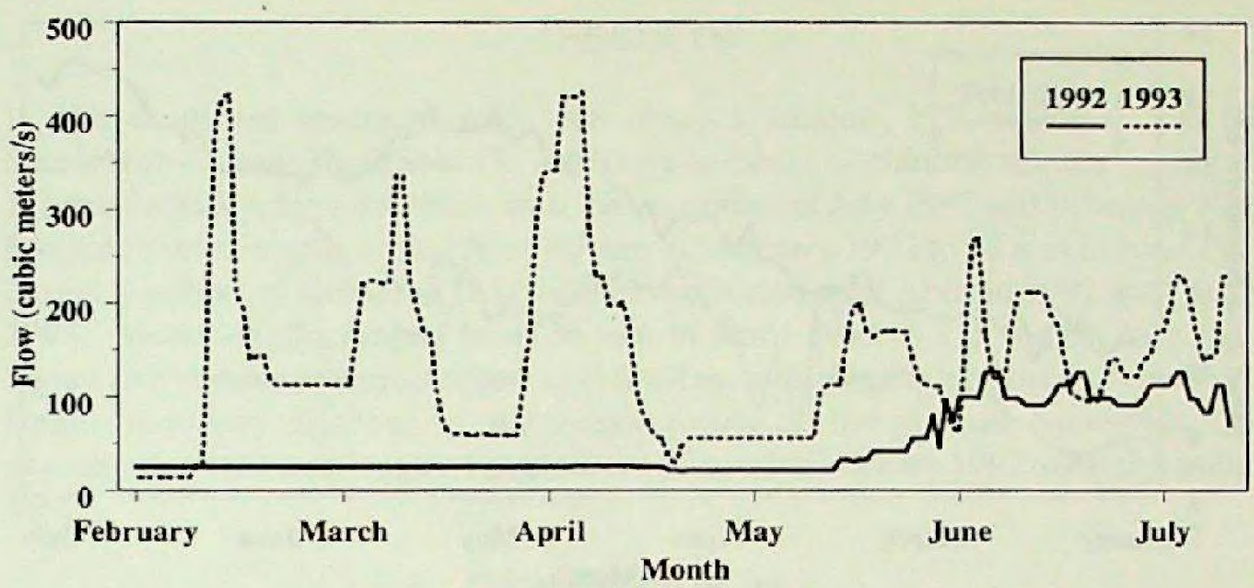

Figure 1. Lower American River mean daily flow from 1 February to 15 July 1992 and 1993. Data provided by California Department of Fish and Game.

were selected because of their accessibility and because they typified the LAR's habitats. We collected fish during the first week of each month between 0900 and 1500 with a 15 x 2-m bag seine with 3-mm square mesh. Our monthly target sample sizes were at least 14 chinook salmon, 14 steelhead, and 12 squawfish, which were based on preliminary stomach analysis (see Hurturbia 1973). Fish were immediately preserved in 10% formalin and transported to the laboratory for analysis. The fork length of each fish was measured to the nearest millimeter and stomach contents were removed, sorted under a dissecting microscope, and weighed to the nearest 0.001 g. For squawfish, which lack a distinct stomach, we analyzed contents in the anterior portion of the alimentary tract from the esophagus to the first bend. Food items were identified to order or family with the aid of Merritt and Cummins (1984), Wang[4] (1986), and Pennak (1989). Food habits data for each species were pooled on a monthly basis and initially analyzed by frequency of occurrence, numeric, and gravimetric (dry weight) methods (Bowen 1983). To assess the relative importance of food items, we calculated an index of relative importance (IRI) for each food category, as described by Hyslop (1980):

$$IRI = (FN + FW)\,FO,$$

where

FN = a food item's percentage of the total number of organisms ingested,
FW = a food item's percentage of the total weight of food ingested, and
FO = a food item's percentage frequency of occurrence in all stomachs examined that contained food.

[4] Wang, J. 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: A guide to the early life histories. Technical Report No. 9, California Department of Water Resources, Sacramento, California, USA.

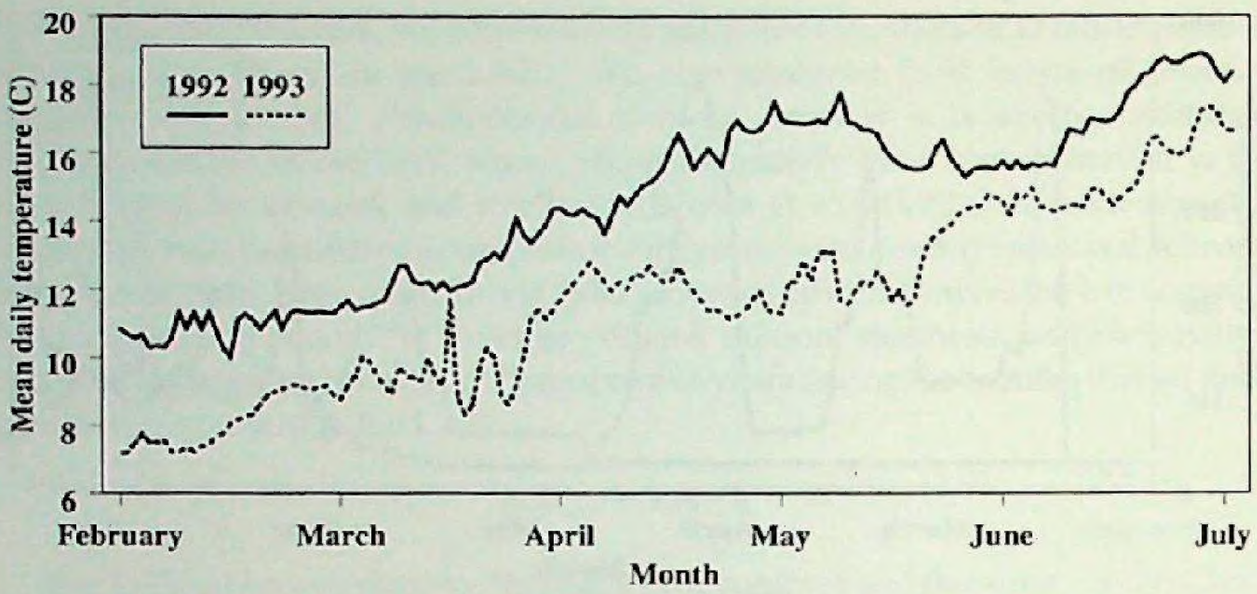

Figure 2. Lower American River mean daily temperature from 15 February to 15 July 1992 and 1993. Data provided by California Department of Fish and Game.

To make dietary comparisons, we converted the IRI values of each food item to percentages based on total IRIs for each month. Food items that occurred in fewer than 5% of the stomachs were not included in the IRI calculations. We calculated an overall index of fullness for each monthly sample by dividing the mean weight of stomach contents for that month by the mean fork length of all fish examined that contained food and multiplying this value by 100. We used one-tailed Mann-Whitney U tests ($\alpha = 0.05$) to compare mean indices of fullness between years.

To analyze dietary similarity among the three species, we calculated Morisita's index of overlap, described by Horn (1966):

$$C_x = \frac{2\sum_{i=1}^{s} x_i y_i}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2}$$

where

C_x = overlap coefficient,

x_i = proportion of the total diet of fish species x contributed by the food category i, and

y_i = proportion of the total diet of fish species y contributed by food category i.

A C_x value of 0 would indicate no food categories in common, while 1.0 would indicate identical diets. Zaret and Rand (1971) assumed a value ≥ 0.6 indicated significant overlap, which we also used for our comparisons.

RESULTS

We examined stomachs from 468 chinook salmon, 227 steelhead, and 337 Sacramento squawfish (Table 1). Adequate numbers of chinook salmon (minimum 14) were collected in all months with the exception of July 1992 and February 1993. Monthly mean lengths varied from 40 mm in February 1992 to 72 mm in June 1992. Target numbers of steelhead (14) were not collected until April in 1992 and May in 1993. Mean lengths ranged from 36 mm in April 1992 to 112 mm in July 1992. Squawfish numbers were adequate (12) in all months. On the basis of their unimodal length-frequency distribution, we judged nearly all the juvenile squawfish to be yearlings whose mean lengths ranged from 50 mm in February 1992 to 88 mm in June 1992.

Composition of Diets

Chinook salmon and steelhead utilized a variety of food items, but the major portion of their diet was composed of only a few taxa of aquatic insects. In 1992, major food items of chinook salmon were chironomid pupae, larvae, and adults; baetid adults; and hydropsychid larvae and pupae (Table 2). Their diet was less

Table 1. Monthly sample size and mean fork lengths (FL) of chinook salmon, steelhead, and Sacramento squawfish juveniles, lower American River, 1992 and 1993.

Species	Year		February	March	April	May	June	July
Chinook salmon	1992	Sample size	45	47	44	41	38	
		Mean FL	40	44	56	63	72	
		SD	8	10	13	8	9	
	1993	Sample size		53	66	64	49	21
		Mean FL		39	50	55	55	69
		SD		4	7	11	9	9
Steelhead	1992	Sample size			38	23	45	21
		Mean FL			36	89	82	112
		SD			2	7	8	10
	1993	Sample size				32	36	32
		Mean FL				43	56	61
		SD				8	10	15
Sacramento squawfish	1992	Sample size	18	31	48	27	30	45
		Mean FL	50	60	64	76	88	85
		SD	10	33	16	32	42	31
	1993	Sample size	12	20	46	22	22	16
		Mean FL	62	59	66	63	78	86
		SD	4	9	11	12	15	17

varied in 1993 when they fed primarily on chironomids. In general, chinook salmon fed on a greater diversity of items as the year progressed in 1992 (Fig. 3) but, in 1993, salmon fed primarily on chironomids in all months except February. Steelhead feeding followed a similar pattern in 1992, when baetid adults and nymphs and hydropsychid larvae were major food items; these items were uncommon in 1993 when chironomids were the major food every month (Fig. 4). In both years, terrestrial arthropods and fish larvae were uncommon in the diets of both chinook salmon and steelhead.

Sacramento squawfish fed mainly on aquatic insects in both years, primarily corixid adults and chironomid larvae; baetid adults and hydropsychid larvae also were prominent on the diet in 1992 (Table 2). Seasonally, chironomids decreased in importance from late winter through spring, while corixids increased in importance and by May had become a major food item (Fig. 3). Fish (Sacramento sucker larvae) were a common food item only in May 1993. Terrestrial arthropods (arachnids and formicids) were occasionally eaten, although these items formed a substantial part of the diet only in March 1993, when their collective IRI% was 44. Less common food items were lumbricids, decapods, and dytiscids.

Table 2. Major food items of juvenile chinook salmon, steelhead, and Sacramento squawfish in the lower American River, 1992-1993. Numbers represent percent index of relative importance (IRI%) for each year.

		Year	
Species	Prey Item	1992	1993
	Baetid adults	20%	
	Hydropsychid larvae & pupae	12%	
Chinook	Chironomid larvae	11%	40%
salmon	Chironomid pupae	50%	54%
	Chironomid adults		3%
	Other	7%	3%
	Baetid nymphs	6%	
	Baetid adults	75%	
Steelhead	Hydropsychid larvae	14%	
	Chironomid larvae		67%
	Chironomid pupae		29%
	Other	5%	4%
	Baetid adults	7%	
	Hydropsychid larvae	5%	
Sacramento	Corixid adults	66%	40%
squawfish	Chironomid larvae	13%	21%
	Chironomid adults		10%
	Fish larvae		23%
	Other	9%	7%

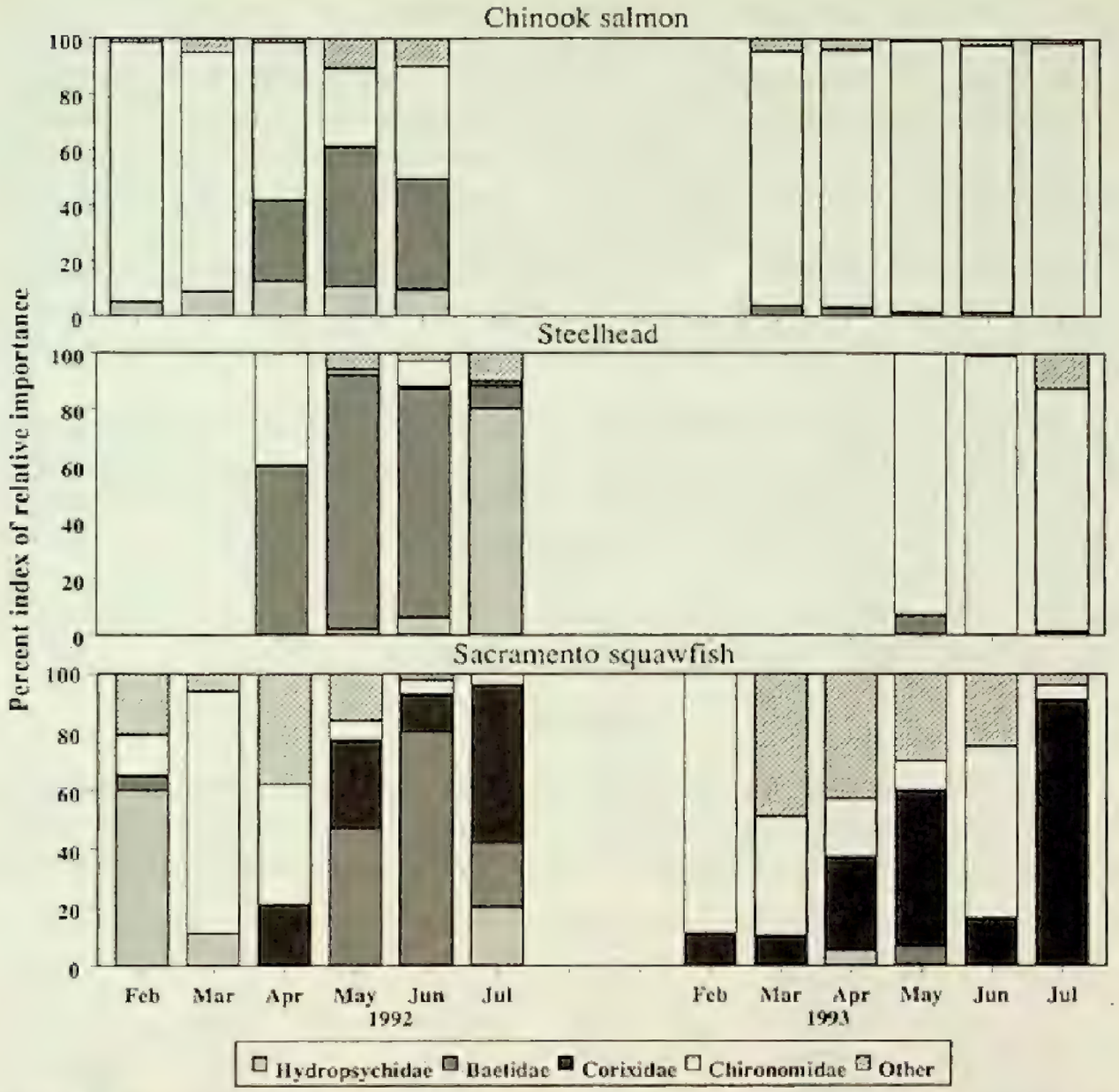

Figure 3. Major food items of chinook salmon, steelhead, and Sacramento squawfish in the lower American River by month, 1992 and 1993. Food items are represented by percent index of relative importance (IRI%) for each month.

Dietary Overlap

The diet of Sacramento squawfish did not significantly overlap ($C_s < 0.6$) with that of either chinook salmon or steelhead (Fig. 4). The greatest similarity between the squawfish and chinook salmon diet occurred in March 1992, when both species fed heavily on chironomids. The greatest similarity between squawfish and steelhead was in July 1992, when baetids were a common food item for both species.

Greater overlaps occurred between chinook and steelhead, especially in June 1992 and May and June 1993 (Fig. 4). In 1992, baetids constituted the major food item by weight for both species, while in 1993 chironomids (both larvae and pupae) formed the bulk of the diet for both species in these months.

Feeding Activity

Patterns of feeding activity of chinook salmon and steelhead, as revealed by occurrence of empty stomachs and quantity of food in stomachs, varied with season as well as year. We found few empty chinook salmon or steelhead stomachs in either year (Table 3). However, feeding activity was greater for these species in 1992, as mean index of fullness was significantly higher that year for both chinook ($U = 21.5$, $P = 0.028$) and steelhead ($U = 12.0$, $P = 0.016$). The index of fullness for both species generally increased into spring in 1992, while a seasonal trend was less apparent in 1993. The high index of fullness for steelhead in May of 1992 resulted from heavy feeding on adult baetids.

Sacramento squawfish feeding activity was similar both years, although seasonal feeding patterns differed. Thirty-eight percent of squawfish stomachs were empty in 1992 compared to 47% in 1993, but this difference was not statistically significant ($\chi^2 = 3.66$, $P = 0.056$) (Table 3). Mean indices of fullness also were not significantly different between years ($U = 26.5$, $P = 0.077$). In 1992, occurrence of empty stomachs declined as the season progressed, while index of fullness increased. A seasonal increase in feeding activity was not apparent in 1993.

DISCUSSION

The diets of juvenile chinook salmon, steelhead, and Sacramento squawfish in the LAR, composed mainly of immature stages of aquatic insects, were generally similar to those reported for these species by other workers (Shapovalov and Taft 1954,

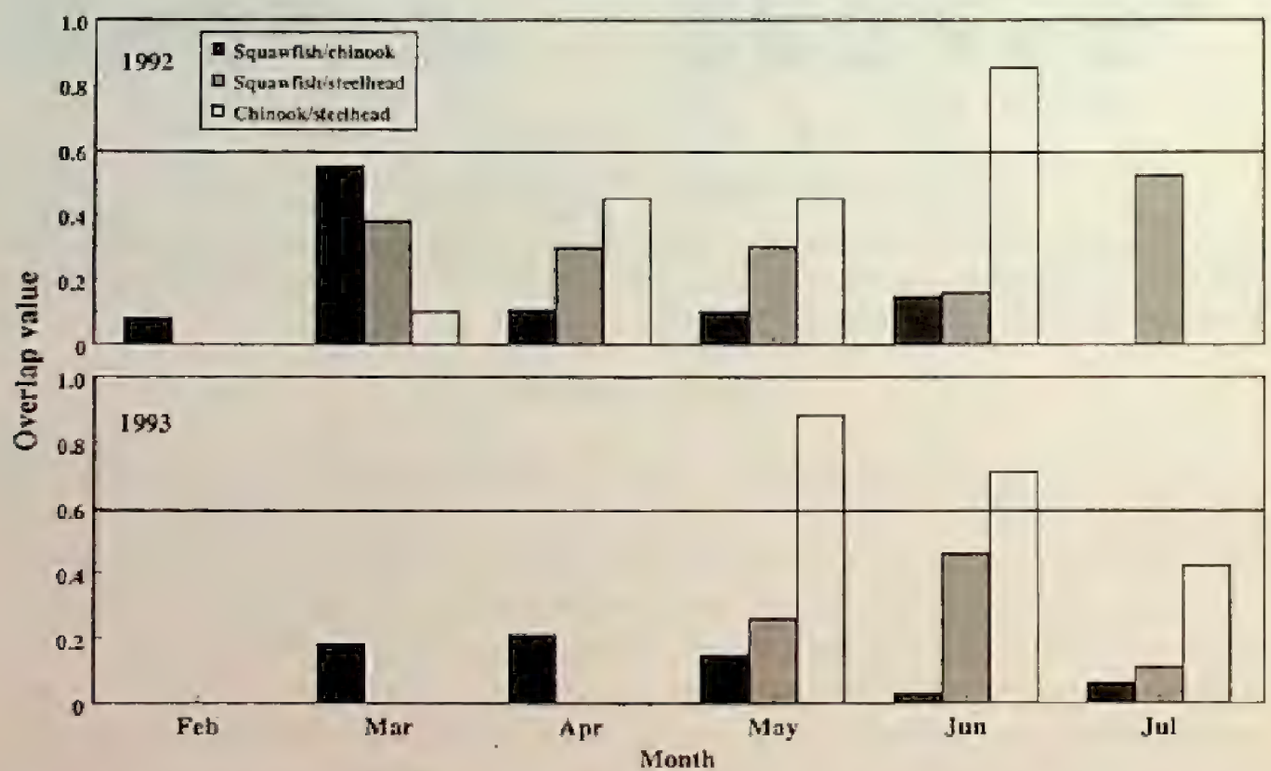

Figure 4. Morisita's overlap indices, by month, for diets of juvenile chinook salmon, steelhead, and Sacramento squawfish from the lower American River, 1992 and 1993. Solid horizontal line indicates level of significant overlap.

Becker 1973, Moyle 1976, Johnson and Johnson 1981, Sagar and Glova 1988, Brown 1990, Power 1992). The low dietary overlap of squawfish with chinook and steelhead was due in part to the importance of corixids in the squawfish diet. Corixids were rare or absent in drift and Surber samples from the LAR (Green[5] 1976, Merz[6] 1993), but were commonly observed in shallow areas of slow current near shore, especially around filamentous algae. In contrast, major food items of chinook and steelhead (baetid nymphs, chironomid larvae, and hydropsychid larvae) were common in drift and Surber samples in swift water (Green[5] 1976, Merz[6] 1993). This observation agrees with Moyle (1976) who described juvenile chinook salmon as opportunistic drift feeders. Thus, the lack of dietary overlap between squawfish and these two

Table 3. Monthly feeding patterns of juvenile chinook salmon, steelhead, and Sacramento squawfish, lower American River, 1992-1993, as indicated by frequency of empty stomachs and index of fullness (IF). Parentheses indicate numbers of stomachs containing food.

		1992		1993	
Species	Month	% Empty Stomachs	IF	% Empty Stomachs	IF
Chinook salmon	February	0 (45)	0.8		
	March	4 (45)	2.1	4 (51)	1.0
	April	2 (43)	3.4	0 (66)	0.8
	May	0 (41)	2.7	5 (61)	1.1
	June	5 (36)	3.3	8 (45)	1.0
	July			0 (21)	0.4
	$\bar{X} \pm$ SD	2 ± 2	2.5 ± 1.1	3 ± 3	0.9 ± 0.3
Steelhead	April	3 (37)	1.0		
	May	0 (23)	7.1	6 (30)	0.6
	June	0 (45)	2.5	0 (36)	0.8
	July	0 (21)	3.7	3 (31)	0.9
	$\bar{X} \pm$ SD	1 ± 2	3.6 ± 2.6	3 ± 3	0.8 ± 0.2
Sacramento squawfish	February	67 (6)	0.4	33 (8)	0.2
	March	61 (12)	0.2	55 (9)	0.2
	April	50 (24)	1.1	43 (26)	1.0
	May	19 (22)	0.7	64 (8)	0.2
	June	13 (26)	1.5	32 (15)	0.2
	July	20 (36)	1.4	56 (7)	1.4
	$\bar{X} \pm$ SD	38 ± 24	0.9 ± 0.5	47 ± 14	0.5 ± 0.5

[5] Green, D.B. 1976. Comparison of benthic macroinvertebrates above and below a storm drainage-sewage outfall in the American River, Sacramento, California. M.S. Thesis, California State University, Sacramento, California, USA.

[6] Merz, J.E. 1993. A survey of drift and benthic communities and their use in the diet of the more abundant fish species in the lower American River, February-July, 1992. California State University, Sacramento, Foundation Contract Report FG1353.

salmonids is likely due to differences in their specific feeding locations. The dietary overlap between chinook salmon and steelhead was highest in May and June, the time when steelhead juveniles were most abundant and chinook salmon juveniles were decreasing in abundance due to downstream migration.

The contrasting environmental conditions of the LAR between 1992 and 1993, namely of flow variability and water temperature, resulted in different feeding patterns, at least for chinook salmon and steelhead. Highly fluctuating water levels and lower water temperatures in 1993 probably were responsible for the reduced feeding that year. Variable flows are generally detrimental to benthic invertebrates (Ward 1976, Petts 1984). Fluctuating discharges from a hydroelectric dam on the Connecticut River reduced macroinvertebrate populations in substrates that were repeatedly exposed (Fisher and LaVoy 1972); only chironomids were found in the zone that experienced the greatest exposure. Thus, it is not surprising that LAR chinook salmon, steelhead, and squawfish (particularly the former two species) greatly increased their utilization of chironomids in 1993.

In summary, our data support the hypothesis that fluctuating water levels during the salmonid nursery period inhibit feeding of chinook salmon, steelhead, and possibly Sacramento squawfish. Future studies are needed on responses of macroinvertebrate populations to levels of river discharge and degree of water fluctuations and how changes in dietary patterns of fishes affect growth and survival.

ACKNOWLEDGMENTS

We thank W. Snider, California Department of Fish and Game, for his support on this project and his LAR crew for assistance in field collections; W. Fields, Hydrozoology, Inc. and W. Shepard, California State University, Sacramento, for verification of insect identifications; and D. Faoro for use of his computer program on calculation of dietary overlap. We also thank L. Brown, U.S. Geological Survey; P. Moyle, University of California, Davis; D. Kohlhorst, California Department of Fish and Game; and two anonymous reviewers whose critical reviews greatly improved the manuscript.

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Received: 17 August 1995
Accepted: 22 June 1996

California Fish and Game 82(4):160-174 1996

EFFECTS OF AQUACULTURE ON HABITAT USE BY WINTERING SHOREBIRDS IN TOMALES BAY, CALIFORNIA

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We measured abundances of wintering shorebird species simultaneously on four control plots and two aquaculture plots from November 1989 to February 1994 on tidal flats in Tomales Bay, California. Twelve abundance estimates for each plot were obtained each year. We used analysis of covariance to model the results, controlling for the presence of roosting gulls that may have displaced foraging shorebirds. The analysis included effects related to intraseasonal timing, annual variation, and the presence of aquaculture. The two most abundant shorebird species in Tomales Bay, western sandpiper, *Calidris mauri*, and dunlin, *Calidris alpina*, significantly avoided aquaculture areas. Willets, *Catoptrophorus semipalmatus*, however, were attracted to aquaculture plots. Four other species showed no preferences for control or aquaculture plots. Evidence of underlying (pre-existing) habitat conditions did not explain these results. We found no differences in species richness or Shannon diversity index between control and aquaculture areas. Our results suggest a net decrease in total shorebird use in areas developed for aquaculture.

INTRODUCTION

Shorebirds generally concentrate where feeding efficiency is greatest (Goss-Custard 1970, Connors et al. 1981; reviews by Evans and Dugan 1984, Meire and Kuyken 1984, Puttick 1984) and invertebrate prey density (Goss-Custard et al. 1977, Bryant 1979, Wilson 1990, Colwell and Landrum 1993) or availability (Recher 1966, Myers et al. 1980, Goss-Custard 1984) is highest. Sediment characteristics can influence shorebird distribution and density by affecting prey density or availability (Page et al. 1979, Quammen 1982, Yates et al. 1993). Foraging distributions and densities of shorebirds are also influenced by other macrohabitat (Burger 1984a) and microhabitat characteristics (Recher 1966, Baker and Baker 1973, Gerstenberg 1979, Burger 1984b). In some species, social behavior determines the extent to which habitat characteristics or food availability influence numbers of shorebirds using a particular area (Myers 1984).

Pacific oyster, *Crassostrea gigas*, culture alters spatial habitat structure by introducing shellfish, racks, stakes, culture bags, marker poles, and other equipment onto open tidal flats. Research conducted to date on ecosystem effects of oyster

culture has been limited to studies of effects on sediment (Ottmann and Sornin 1985, Deslous-Paoli et al. 1992) and benthic infauna (Triani[1] 1994); effects of oyster culture on bird populations have not been addressed. Therefore, from 1989 to 1994, we investigated the use of intertidal mud flats by wintering shorebirds in relation to Pacific oyster growing operations at Walker Creek Delta, Tomales Bay, California. Study objectives were to (i) test for selection or avoidance of aquaculture areas by wintering shorebirds, (ii) test for differences in shorebird diversity between open tidal flats and aquaculture areas, (iii) examine temporal and spatial variation of shorebird abundance on open tidal flats and aquaculture areas, and (iv) compare intraseasonal shifts in use of tidal flats and aquaculture areas with overall abundance changes in Tomales Bay.

STUDY AREA AND METHODS

We conducted the study on test plots at Walker Creek Delta near the north end of Tomales Bay, California (Fig. 1). Tidal flats on the delta were composed of consolidated fine sands, silts, and clays (Daetwyler 1966) and were divided by three creek channels. We marked six study plots around the perimeter of the delta, each plot occupying 225 meters of shoreline and covering approximately 2 ha of tidal flat between 0.0 and 0.3 m above mean lower low water (MLLW) (Fig. 1). Two control plots (Plots 1 and 2) were on the south perimeter of the delta. Two others (Plots 3 and 4) were designated as treatment plots on currently used aquaculture lease areas (Fig. 1). We established Plots 5 and 6 on undeveloped aquaculture areas to provide temporal experimental control as they were developed for aquaculture; however, aquaculture development did not occur as expected. Instead, local oyster growers developed an area that included approximately 15% of Plot 6 by the end of the 1992-93 sampling period (Fig. 1). This aquaculture operation was abandoned subsequently and the aquaculture equipment was removed prior to the 1993-94 sampling period. Control and aquaculture test areas were separated by at least 100 m; within control and aquaculture areas, plots were separated by 50 m.

Oyster growers used 0.61 x 0.91-m black plastic mesh bags placed on the bottom and 0.30 to 0.61 m above the bottom on 1.22 x 2.44-m steel re-bar frames supported by PVC pipe legs. The ends of rows of oyster bags were often marked with 1 to 2.5-m-high PVC stakes.

We conducted three counts per month on each plot, from November through February 1989-90 to 1993-94. Count days were clustered in groups of three, usually consecutive days during spring tides. Three observers, each observing two plots, used telescopes to conduct simultaneous counts of all shorebirds on the six study plots. Observers rotated among pairs of plots on successive days. Each count period consisted of three 20-min counts initiated at 30-min intervals as the edge of the falling tide receded through the study plots; shorebirds generally foraged near the edge of the falling tide (Recher 1966, Evans and Dugan 1984). We recorded the peak number

[1]Triani, M. 1994. Influence of oyster culture methods on benthic infauna of Humboldt Bay, California. Draft M.S. Thesis, Humboldt State University, Arcata, California, USA.

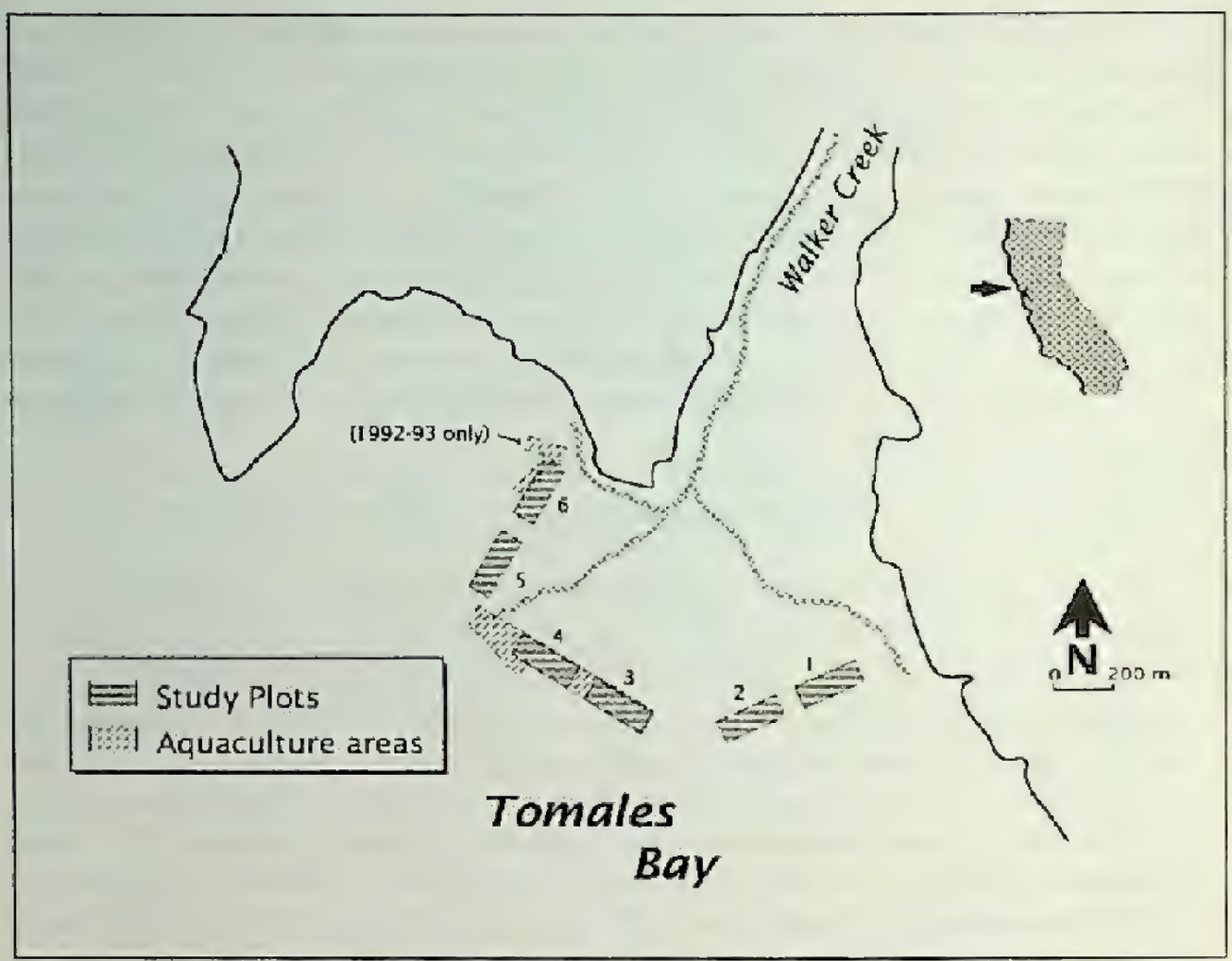

Figure 1. Shorebird study plots and aquaculture lease areas of Walker Creek Delta, Tomales Bay, California. Gray lines show the stream channels.

of birds of each species seen in each plot during each 20-min count interval. Abundances from the three count intervals were averaged to provide an index of shorebird use. We did not estimate absolute density because of increasing exposure of suitable foraging habitat as the water level receded.

To account for possible population effects on annual and intraseasonal differences in habitat use, we compared results with Tomales Bay-wide counts (Kelly[2] 1990-94). We conducted three Tomales Bay-wide counts in early winter (November-December) and three in late winter (15 January - 28 February) each year. We generally scheduled Tomales Bay-wide counts within 3-7 days of plot counts. Kelly[3] (1990) described the census methods.

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[2] Kelly, J.P. 1990-94. Annual report of the Tomales Bay shorebird census. ACR Project Reports 89-4-1, 89-4-2, 89-4-3, 89-4-4, and 89-4-5, Audubon Canyon Ranch, Stinson Beach, California, USA.

[3] Kelly, J.P. 1990. 1989-90 winter and spring shorebird abundances on Tomales Bay, California, and notes on the movements of shorebirds within Tomales Bay. ACR Project Report 89-4-1, Audubon Canyon Ranch, Stinson Beach, California, USA.

Statistical Analysis

We used a mixed-model analysis of covariance (ANCOVA), controlling for displacement of shorebirds by roosting gulls, to model patterns of abundance. Prior to the analysis, the plot counts were log-transformed to normalize the data. Aquaculture treatment (presence or absence) and intraseasonal timing (early vs. late winter) were considered to be fixed effects; plots (nested within control and aquaculture areas) and years were considered to be random effects. We used this same analysis method to examine species diversity within plot counts, based on the Shannon index (Magurran 1988). We tested for associations between the abundance of gulls and shorebirds on the study plots using correlation analysis.

We investigated the possibility that habitat use gradients occur on the delta by using ANCOVA to test for differences (fixed effects) between (i) control plots on the northwest (Plots 5 and 6) and southeast (Plots 1 and 2) sides of the delta and (ii) control plots on the inner (Plots 1 and 6) and outer (Plots 2 and 5) portions of the delta (Fig. 1). We examined the possible influence of the partial use of Plot 6 for aquaculture on shorebird abundance by using ANCOVA to test for differences (fixed effects) between (i) Plot 6 in 1992-93 and the other 4 years of study, and (ii) Plot 6 and the other control plots in 1992-93. Further, ANCOVA models generated for each species were repeated after removing the 1992-93 Plot 6 data and examined for differences in the significance levels of individual effects.

A maximum likelihood approach was used to estimate parameters of the ANCOVA models (BMDP Program 3V; Dixon 1992). The significance of each source of variation was tested with a likelihood ratio chi-square comparing the original model with a submodel in which the associated parameter was set to zero.

RESULTS

While completing 360 shorebird plot counts, we observed dense concentrations of gulls roosting on Walker Creek Delta. The maximum number of gulls observed within a plot was 7,400; the median was 65. Of all gulls observed on study plots, 76.6% were California gulls, *Larus californicus*; 18.2% were western, *Larus occidentalis*, or glaucous-winged gulls, *Larus glaucescens*; 5.4% were ring-billed gulls, *Larus delawarensis*; and 0.8% were mew gulls, *Larus canus*. The number of gulls occupying study plots was inversely related to the number of marbled godwits, *Limosa fedoa* ($r = -0.15$, $P < 0.01$); western sandpipers, *Calidris mauri* ($r = -0.20$, $P < 0.001$); least sandpipers, *Calidris minutilla* ($r = -0.21$, $P < 0.001$); dunlins, *Calidris alpina* ($r = -0.26$, $P < 0.001$); willets, *Catoptrophorus semipalmatus* ($r = -0.12$, $P < 0.05$); and all shorebirds combined ($r = -0.25$, $P < 0.001$). Correlations of gull abundance with black-bellied plover, *Pluvialis squatarola* ($r = -0.08$), and sanderling, *Calidris alba* ($r = -0.04$) were negative, but not significant ($P > 0.05$).

It is not likely that these relationships resulted from differences in habitat use because gulls and shorebirds used the same areas and we obtained similar results in separate within-plot analyses. The negative signs of correlation coefficients between gulls and all seven species of shorebirds analyzed in this paper suggest that roosting

gulls displaced shorebirds in areas of otherwise suitable shorebird habitat. Therefore, we used ANCOVA to control for the effects of roosting gulls on the use of control and aquaculture plots by shorebirds.

Oyster workers were present on aquaculture areas during 62% of our counts, suggesting that human activity might have influenced bird distributions. However, the distribution of gulls on the delta was not related to the presence of oyster workers (likelihood ratio = 0.58, $P > 0.45$) or developed aquaculture areas (likelihood ratio = 0.001, $P > 0.97$). We observed no movements of shorebirds into or out of plots in response to human activity and the distributions of shorebirds were not significantly related to the presence of oyster workers on aquaculture plots (ANCOVA; $P = 0.11$, 0.59, 0.89, 0.10, 0.49, 0.68, 0.17 for black-bellied plover, willet, marbled godwit, sanderling, western sandpiper, least sandpiper, and dunlin). The most abundant shorebird species we observed was dunlin, followed by least sandpiper and western sandpiper (Table 1). Sanderlings and larger shorebirds such as marbled godwits and willets were less abundant. Greater yellowlegs, *Tringa melanoleuca*; ruddy turnstones, *Arenaria interpres*; black turnstones, *Arenaria melanocephala*; short-billed dowitchers, *Limnodromus griseus*; and long-billed dowitchers, *Limnodromus scolopaceus*, each occurred on less than 10% of plot counts.

Data for seven species were adequate for parametric tests of the hypothesis that abundance on aquaculture and control areas did not differ (Table 2). Use of control and aquaculture areas by black-bellied plovers, marbled godwits, sanderlings, and least sandpipers was not significantly different than expected by chance, given the underlying variation among the nested plots ($P > 0.05$) (Tables 1 and 2). However, western sandpipers and dunlins were significantly less abundant ($P < 0.05$) and willets significantly more abundant ($P < 0.001$) on aquaculture plots than on control plots.

A significant difference in the use of all study plots by willets between early and late winter (Table 2: Seasons) resulted primarily from mid-season influxes onto aquaculture plots (Table 1; $F = 29.92$, $df = 1, 118$, $P < 0.001$). Smaller early-to-late winter increases of willets occurred on control plots (Table 1; $F = 9.46$, $df = 1, 238$, $P = 0.002$). We found no general baywide intraseasonal increase (pooled across years) in willet numbers on Tomales Bay ($F = 1.75$, $df = 1, 27$, $P = 0.20$) and no significant baywide intraseasonal differences were found within individual years (F values for all years not significant: $P > 0.05$; Kelly[2] 1990-94).

A significant early-to-late winter difference in the use of study plots by marbled godwits (Table 2) also resulted from mid-season increases on aquaculture plots (Table 1; $F = 8.23$, $df = 1,118$, $P = 0.005$); early-to-late winter differences on control plots were not significant (Table 1; $F = 0.58$, $df = 1, 238$, $P = 0.45$). We found no general baywide intraseasonal increase (pooled across years) in number of marbled godwits ($F = 0.56$, $df = 1,27$, $P = 0.46$); within years, marbled godwits increased only in 1990-91 ($F = 35.04$, $P < 0.01$, $df = 1,3$; Kelly[2] 1990-94).

Interactions between areas, seasons, and years accounted for some of the variability of shorebird abundance. Differences in abundance of black-bellied plovers, willets, and least sandpipers between control and aquaculture areas were partly dependent on winter timing (Table 2: Areas x Seasons). Differences in

Table 1. Means and 95% confidence intervals of means (L_1 - L_2) of shorebird abundances on study plots from 1989-90 to 1993-94 at Walker Creek Delta, Tomales Bay, California; n = 116 and 124 on early winter (EW) and late winter (LW) control plots and 58 and 62 on EW and LW aquaculture plots. Confidence intervals are asymmetric because values are transformed back into linear scale from log-transformed data.

		Control		Aquaculture	
Species	Season	Mean	L_1 - L_2	Mean	L_1 - L_2
Black-bellied Plover	EW	0.91	0.65 - 1.22	1.36	0.81 - 2.08
	LW	0.99	0.71 - 1.32	0.43	0.23 - 0.68
Greater Yellowlegs	EW	0.00	0.00 - 0.00	0.02	-0.01 - 0.06
	LW	0.00	0.00 - 0.00	0.00	0.00 - 0.00
Willet	EW	0.42	0.20 - 0.58	1.45	0.87 - 2.20
	LW	0.84	0.63 - 1.08	5.03	4.01 - 6.27
Marbled Godwit	EW	2.44	1.53 - 3.66	1.27	0.57 - 2.28
	LW	3.01	2.10 - 4.19	4.15	2.39 - 6.81
Ruddy Turnstone	EW	0.02	0.00 - 0.03	0.12	0.05 - 0.20
	LW	0.00	0.00 - 0.02	0.02	0.00 - 0.04
Black Turnstone	EW	0.08	0.03 - 0.13	0.31	0.13 - 0.53
	LW	0.00	0.00 - 0.00	0.02	-0.01- 0.05
Sanderling	EW	1.82	1.14 - 2.72	2.48	1.27 - 4.34
	LW	0.81	0.51 - 1.17	2.09	1.14 - 3.45
Western Sandpiper	EW	23.63	16.28 - 34.10	2.99	1.60 - 5.15
	LW	9.83	6.14 - 15.41	1.80	0.90 - 3.13
Least Sandpiper	EW	36.61	24.98 - 53.44	9.20	4.95 - 16.48
	LW	9.61	6.01 - 15.07	10.86	6.25 - 18.39
Dunlin	EW	111.72	69.88 -178.26	9.12	4.63 - 17.20
	LW	23.24	13.91 - 38.40	5.97	3.09 - 10.88
Long-billed Dowitcher	EW	0.00	0.00 - 0.00	0.00	0.00 - 0.00
	LW	0.05	-0.02 - 0.12	0.00	0.00 - 0.00
Short-billed Dowitcher	EW	0.11	0.03 - 0.20	0.09	0.01 - 0.17
	LW	0.00	0.00 - 0.01	0.01	0.01 - 0.02
Dowitcher (Grouped)	EW	0.12	0.05 - 0.20	0.37	0.13 - 0.65
	LW	0.02	-0.01- 0.05	0.12	0.02 - 0.23
Gull species (Covariate)	EW	64.22	43.49 - 94.62	160.99	112.23 - 230.75
	LW	154.27	113.37 - 209.80	74.91	49.89 - 112.24

Table 2. Components of variation of log-transformed winter shorebird abundance at Walker Creek Delta, Tomales Bay, California. Analysis of covariance was used to control for the displacement of shorebirds by gulls. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Source of Variation	Black-bellied Plover	Willet	Marbled Godwit	Sanderling	Western Sandpiper	Least Sandpiper	Dunlin
AREAS (control vs. aquaculture)							
Parameter Estimate	0.014	-0.189	0.016	-0.080	0.344	0.126	0.395
Standard Error	0.032	0.036	0.060	0.121	0.154	0.181	0.125
Likelihood Ratio χ^2 (df = 1)	0.183	10.952***	0.069	0.427	3.914*	0.479	6.159*
PLOTS (nested within AREAS)							
Parameter Estimate	0.002	0.004	0.009	0.038	0.076	0.099	0.025
Standard Error	0.002	0.003	0.009	0.028	0.056	0.071	0.025
Likelihood Ratio χ^2 (df = 1)	2.654	7.661**	4.586*	35.753***	27.331***	32.703***	4.108*
YEARS							
Parameter Estimate	0.041	0.002	0.143	0.065	0.035	0.000	0.285
Standard Error	0.028	0.009	0.102	0.074	0.073	0.000	0.240
Likelihood Ratio χ^2 (df = 1)	11.703***	0.081	6.442*	1.169	0.288	0.000	3.286
SEASONS (early vs. late winter)							
Parameter Estimate	0.041	-0.132	-0.124	0.052	0.118	0.114	0.185
Standard Error	0.024	0.038	0.050	0.035	0.070	0.050	0.090
Likelihood Ratio χ^2 (df = 1)	2.575	7.030**	4.082*	1.826	2.281	3.745	3.119

Table 2. Continued.

Source of Variation	Black-bellied Plover	Willet	Marbled Godwit	Sanderling	Western Sandpiper	Least Sandpiper	Dunlin
AREAS X SEASONS							
Parameter Estimate	-0.062	0.062	0.059	0.044	0.035	0.125	0.103
Standard Error	-0.024	0.022	0.036	0.027	0.054	0.046	0.048
Likelihood Ratio χ^2 (df = 1)	5.319*	5.465*	2.141	2.706	0.404	6.045*	3.520
AREAS X YEARS							
Parameter Estimate	0.000	0.001	0.006	0.068	0.066	0.121	0.088
Standard Error	0.000	0.005	0.015	0.051	0.067	0.070	0.073
Likelihood Ratio χ^2 (df = 1)	0.000	0.063	0.177	9.307**	1.819	7.168**	3.192
SEASONS X YEARS							
Parameter Estimate	0.000	0.010	0.012	0.006	0.020	0.005	0.059
Standard Error	0.000	0.010	0.017	0.007	0.035	0.014	0.049
Likelihood Ratio χ^2 (df = 1)	0.000	2.185	0.648	1.210	0.318	0.195	2.083
AREAS X SEASONS X YEARS							
Parameter Estimate	0.006	0.004	0.008	0.000	0.023	0.000	0.000
Standard Error	0.004	0.006	0.016	0.000	0.035	0.000	0.000
Likelihood Ratio χ^2 (df = 1)	4.496*	1.108	0.495	0.000	0.883	0.000	0.000
GULLS: Covariate							
Parameter Estimate	-0.018	-0.057	-0.073	0.016	-0.087	-0.156	-0.112
Standard Error	0.023	0.023	0.041	0.038	0.060	0.065	0.066
Likelihood Ratio χ^2 (df = 1)	0.599	5.796*	2.996	0.164	1.998	5.599*	2.601

abundance of black-bellied plovers and marbled godwits between control and aquaculture areas were partly dependent on differences among years (Table 2: Areas x Years). Winter timing influenced the abundance of black-bellied plovers on control and aquaculture areas differently among years (Table 2: Areas x Seasons x Years).

Comparisons of shorebird abundance among control plots showed no underlying habitat gradients and additional analyses using subsets of controls were consistent with our initial results. Habitat use did not differ between the inner (Plots 1 and 6) and outer (Plots 2 and 5) portions of the control area for all species analyzed (P ranged from 0.45 to 0.88), except for sanderlings, which were significantly more abundant on outer control plots than on inner control plots (likelihood ratio = 4.11, $P = 0.043$). Habitat use by black-bellied plover, willet, marbled godwit, sanderling, and dunlin did not differ between the northwest and southeast sides of the delta (P ranged from 0.06 to 0.88). Western sandpipers and least sandpipers used the northwest side of the delta significantly more than the southeast side (likelihood ratios = 6.78 and 8.53; $P < 0.01$). An additional ANCOVA using only control plots on the southeast side of the delta, where western sandpiper abundance was lower, was consistent with the initial results based on all four control plots, showing significant avoidance of the aquaculture area (likelihood ratio = 8.04, $P < 0.01$). Analysis of covariance using only control plots on the northwest side, and in a separate analysis, only control plots on the southeast side of the delta confirmed the absence of significant aquaculture effects on least sandpiper abundance (likelihood ratios = 2.94 and 0.23, $P > 0.05$). Although dunlin abundance did not differ significantly between control areas on the two sides of the delta (likelihood ratio = 3.52, $P = 0.06$), mean values were higher on the southeast side. Analysis of covariance based only on control plots on the northwest side of the delta confirmed our initial results showing significant avoidance of the aquaculture area by dunlins (likelihood ratio = 4.02, $P = 0.045$).

The presence of aquaculture equipment on up to 15% of Plot 6 in 1992-93 did not influence the overall results. Shorebird abundance on Plot 6 did not differ ($P > 0.05$) between 1992-93 and the other 4 years of study and, except for willets, did not differ ($P > 0.05$) from other control plots in 1992-93. Willets were significantly more abundant on Plot 6 in 1992-93 than on the other control plots (likelihood ratio = 4.19, $P = 0.041$) as a result of the regular occurrence of one individual in the vicinity of the oyster racks (J. Kelly, pers. obs.). Analysis of covariance models generated for each species after removing the 1992-93 Plot 6 data produced the same significant effects as the original analyses. However, the strength of significant aquaculture effects increased; probabilities that the observed aquaculture effects on abundance of western sandpipers, dunlins, and willets were random were further reduced (likelihood ratios = 5.62, 8.13, 15.10; P= 0.022, 0.004, 0.0001; cf Table 2).

Species richness did not differ between control and aquaculture plots (likelihood ratio = 0.007, $P = 0.93$). We also found no significant difference in proportional species diversity, based on the Shannon index, between control and aquaculture plots (likelihood ratio = 0.616, $P = 0.43$).

DISCUSSION

Wintering western sandpipers and dunlins avoided aquaculture areas, whereas willets favored these areas. These differences were not the result of underlying spatial variation detectable among plots nested within areas. However, we must consider the alternative hypothesis that observed differences between control and aquaculture areas resulted from underlying (pre-aquaculture) habitat conditions along a larger habitat gradient. Although our study did not have a complete set of temporal treatments to control for larger spatial effects, aquaculture development on up to 15% of Plot 6 in 1992-93 influenced the strength of the results. Shorebird use of Plot 6 in 1992-93 was not significantly different from other control plots or years, but the higher significance levels that resulted from the removal of 1992-93 Plot 6 data were consistent with our other results, suggesting that aquaculture effects were independent of underlying spatial gradients. We emphasize, however, the need for further corroboration using more complete temporal controls.

Differences in shorebird densities have been related to differences in foraging substrate types (Page et al. 1979; Myers et al. 1980; Quammen 1982, 1984; Hinklin and Smith 1984; Yates et al. 1993). Existing evidence suggests that pre-aquaculture substrates were similar among plots. Before the development of the aquaculture area, surface sediments at Walker Creek Delta were composed of fine sands, silts, and clays; "clayey silts" (> 50% silt; median grain size = 0.004 - 0.063 mm) dominated the entire study area, with transitional occurrences of poorly sorted "sand-silt-clay" (< 50% of each class; median grain size = 0.063 - 0.250 mm) on the southwest edge of the delta, primarily below MLLW (Daetwyler 1966). Therefore, pre-aquaculture substrates could have had an increasing proportion of fine sands on the outer edge of the delta, but primarily below the lower edge (MLLW) of the study plots. Further evidence that possible pre-aquaculture sediment gradients did not affect our results was found in the absence of underlying habitat use gradients between control plots on the inner and outer delta. Substrates did not appear to differ among study plots, although we did not measure sediment characteristics during our study. Some accumulations of very fine unconsolidated material characteristic of oyster pseudofeces (Day et al. 1987) were occasionally observed in the aquaculture plots (J. Kelly, pers. obs.).

Shorebird density and distribution often varies with the density of prey (Goss-Custard et al. 1977, Connors et al. 1981, Hinklin and Smith 1984, Evans and Dugan 1984, Wilson 1990, Colwell and Landrum 1993). However, pre-aquaculture substrate conditions in the vicinity of our study (Daetwyler 1966) may not have been associated with measurable differences in prey species composition, diversity, or density. Johnson (1971) reported that it is rarely possible in Tomales Bay to demonstrate a high correlation between the abundance or distribution of invertebrate species and a specific property of the sediment, such as particle size. Juskevice[4] (1969) found positive correlations in Tomales Bay between the abundance

[4]Juskevice, J.A. 1969. Interspecific correlation and association in benthic marine communities. Ph.D. Dissertation, University of Chicago, Chicago, Illinois, USA.

of a few invertebrate species and particle size, but only within a narrow range of particle sizes. Therefore, existing evidence suggests that significant pre-aquaculture habitat differences between control and treatment plots may not have been detectable. Nevertheless, without more extensive temporal treatment of control areas, our results only suggest that aquaculture effects on shorebirds were independent of underlying spatial habitat differences.

Hypotheses that could explain factors or processes responsible for the observed differences in shorebird abundance between aquaculture and control areas were not tested in this study. Such hypotheses include reduced or increased foraging opportunities related to (i) aquaculture-induced changes in the abundance or availability of preferred prey (Triani[1] 1994); (ii) alteration of foraging substrates related to aquaculture-induced accumulation of pseudofeces or other sediments (Day et al. 1987, Deslous-Paoli et al. 1992); (iii) alteration of foraging substrates associated with foot traffic by oyster growers, maintenance of stakes and bags, or other aquaculture related activities; (iv) selection or avoidance of oyster bags or racks as foraging substrates; (v) differences in opportunities for group foraging or territoriality resulting from the interruption of open foraging areas by oyster bags and racks; or (vi) differences in risk of predation by raptors.

On numerous occasions, we observed least sandpipers foraging on top of oyster bags as well as on sediments below elevated oyster bags; in contrast, western sandpipers and dunlins generally foraged under or between rows of oyster bags. The primary foraging method used by least sandpipers is pecking at the substrate surface (Baker and Baker 1973), which probably involves visual cues. An emphasis on visual searching and surface feeding may allow least sandpipers to exploit the surfaces of oyster bags and racks and may account for the absence of significant differences in their abundance between control and aquaculture areas. In contrast, dunlins (Baker and Baker 1973) and western sandpipers (Recher 1966, Ashmole 1970) forage more often by probing into substrates and may therefore be less suited for feeding on or around oyster bags and racks. These behavioral differences could account for the reduced abundance of western sandpipers and dunlins we observed in the aquaculture area.

Our results suggest that willets preferred areas with aquaculture activity as feeding areas in winter. We often saw willets foraging on or between aquaculture structures, suggesting enhanced foraging opportunities for willets in these areas. Willets are known to use a wide variety of foraging habitats and prey species and may show seasonal changes in diet (Recher 1966, Stenzel et al. 1976, Page et al. 1979, Kelly and Cogswell 1979). Our results also suggest that willets may exploit aquaculture areas to a greater extent as winter progresses, perhaps opportunistically as food availability or competition for food changes among habitat areas.

Western sandpipers or dunlins may be at greater risk of predation by raptors in aquaculture areas than on open tidal flats because of (i) reduced visibility and delayed detection of approaching predators in aquaculture areas, (ii) increased predation pressure related to the use of aquaculture equipment for perches by predators, or (iii) disruption of antipredator flocking behavior (Page and Whitacre 1975,

Kus et al. 1984) related to the interruption of open foraging areas by oyster bags and racks. In spite of these possibilities, foraging least sandpipers remained on the ground beneath elevated oyster racks during attacks by a peregrine falcon, *Falco peregrinus*, (J. Kelly, pers. obs.), suggesting that aquaculture areas provide increased cover that may protect some species from predation.

Several authors have provided evidence that shorebird populations may be limited by foraging opportunities or habitat modification during winter (Baker and Baker 1973; Goss-Custard 1979, 1984; Evans and Pienkowski 1984; Senner and Howe 1984; Goss-Custard et al. 1995). Evans (1991) estimated that most mortality in dunlins (76%) occurs during the nonbreeding season. In our study, avoidance of aquaculture plots by western sandpipers and dunlins substantially outweighed the selection of aquaculture areas by willets (Table 1). If shorebirds are limited by wintering habitat, changes in habitat use may reflect population effects. When we scaled observed differences in shorebird use to population sizes on Tomales Bay (mean baywide winter abundances of 400, 6,033, and 1,851 for willet, dunlin, and western sandpiper; Kelly[2] 1990-94), average decreases in dunlin and western sandpiper on aquaculture plots were 1.52 and 1.18 times greater than the relative increase observed in willets. When scaled to estimated Pacific Flyway populations (70,000, 450,000-600,000, and 1,300,000 for willet, dunlin, and western sandpiper; Page and Gill 1994), the average decrease in dunlin was 2.70-3.51 times greater than the increase in willet, whereas the proportional decrease in western sandpiper, the most abundant shorebird species in the Pacific Flyway, was only 0.30 times the increase in willet. We emphasize that these comparisons are based on rough population estimates and should be interpreted cautiously.

Existing evidence suggests that (i) foraging shorebirds generally concentrate along the edge of the falling or rising tide (Recher 1966, Evans and Dugan 1984); (ii) oyster growers concentrate their operations on intertidal strata with particular tidal exposure regimes, generally below 0.3 m MLLW (pers. obs.); (iii) small losses in the extent or quality of available feeding habitat could result in proportionally greater decreases in wintering shorebird populations (Myers et al. 1979, Goss-Custard 1979, Senner and Howe 1984); and (iv) the two most abundant shorebird species on Tomales Bay (Kelly[2] 1990-94) and other coastal wetlands of the Pacific Flyway (Kjelmyr et al.[5] 1991) significantly avoided areas used for aquaculture on Tomales Bay (this study). Therefore, foraging opportunities for some species may be particularly limited when tide levels coincide with elevational strata preferred for growing oysters. Although willets may forage preferentially in these areas, and species diversity based on proportional abundances is not significantly affected, our results suggest a net decrease in overall shorebird use of open tidal flats developed for aquaculture.

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[5] Kjelmyr, J., G.W. Page, W.D. Shuford, and L.E. Stenzel. 1991. Shorebird numbers in wetlands of the Pacific Flyway: A summary of spring, fall and winter counts in 1988, 1989, and 1990. Report of the Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California, USA.

ACKNOWLEDGMENTS

This study was made possible by the expert field assistance of R. Macdonald, T. Nordbye, D. Reinking, F. Tomlinson, and C. Wood. Valuable help in developing the sampling design was provided by F. Botti, P. Connors, J. Finger, P. Kelly, J. Maron, and G. Page. We thank D. Oman for helpful comments on the statistical analysis and P. Connors, D. Kohlhorst, J. Orsi, and an anonymous reviewer for several suggestions that improved the manuscript. S. Tappen assisted in the preparation of figures and tables. This study was funded by Contracts FG9519, FG1163, and FG3113WM with the California Department of Fish and Game.

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Received: 10 January 1995
Accepted: 9 January 1997

California Fish and Game 82(4):175-181 1996

ROOSEVELT ELK ALONG THE PRAIRIE CREEK DRAINAGE: AN EVALUATION OF ESTIMATING ABUNDANCE AND HERD COMPOSITION

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Roosevelt elk, *Cervus elephus roosevelti*, abundance north of Orick, Humboldt County, California, was estimated using a mark-resight method for individuals that possessed unique scars, pelage, and antler configurations. Estimated population size was 115 (95% CI = 105-134). Calf:cow, yearling bull:cow, and bull:cow ratios were 0.45:1, 0.21:1, and 0.38:1. Monte Carlo simulations using the joint hypergeometric distribution suggest that improvements in the reliability of estimates can be obtained by increasing the number of resight episodes and observing a large proportion of the population. Estimating size of this unhunted population using the mark-resight approach appears to be reliable and cost-effective.

INTRODUCTION

Since at least the 1920s, Roosevelt elk, *Cervus elephus roosevelti*, have been more abundant in Humboldt County than in any other part of California (Harper et al. 1967, McCullough 1969, Mandel and Kitchen[1] 1979). In particular, an area north of Orick, including the riparian-meadow habitat along Prairie Creek, Gold Bluffs Beach, and Boyes Prairie, has frequently been mentioned as supporting abundant populations of Roosevelt elk (Barnes 1925 a, b; Prescott 1925; Dasmann[2] 1964; Harper et al. 1967; Franklin[3] 1968; Lieb[4] 1973; Mandel and Kitchen[1] 1979; Bowyer 1981). In spite of the seeming abundance of elk in this area, there has been no estimate of the population size that is based on objective, repeatable methods and that measures sampling variation. The reason, in part, has to do with the dense vegetation and the apparent difficulty of detecting individuals. The primary objective of my study was to develop a cost-effective protocol for reliably estimating abundance using a mark-resight approach (White1996). I estimated population size and 95% confidence interval

[1]Mandel, R.D. and D. Kitchen. 1979. The ecology of Roosevelt elk in and around Redwood National Park. Redwood National Park Contract PX 8480-8-0045, Arcata, California, USA.

[2]Dasmann, R.F. 1964. Big game of the redwood forest region. National Park Service, Coast Redwood Study, Contract No. NPS-WASO-II-63-(4), Arcata, California, USA.

[3]Franklin, W.L. 1968. Herd organization, territoriality, movements, and home range in Roosevelt elk. M.S. Thesis, Humboldt State University, Arcata, California, USA.

[4]Lieb, J.W. 1973. Social behavior in Roosevelt elk cow groups. M.S. Thesis, Humboldt State University, Arcata, California, USA.

for a population of elk inhabiting approximately 7.4 km^2 along Prairie Creek and Boyes Prairie in Redwoods National and State parks, Humboldt County. Secondly, I documented the age and sex class composition of the population. Thirdly, I conducted Monte Carlo simulations to assess the reliability of the population estimate and to show how changes in the design of a mark-resight protocol may change the reliability of population estimates.

METHODS

I identified unique elk in Boyes Prairie and along Prairie Creek from scars, ear tags, anomalous morphology, or antler dimensions. The area occupied by these elk was determined by locating the two groups of cows and calves at least once a week from October to May (Weckerly[5] 1996). Elk in this area were habituated to humans and could readily be observed at distances of 10-200 m. Male and female elk of all ages were observed in all portions of the area during 52 h of observation on 13 occasions from July to December 1995. At first light (0700) on 24 and 25 January 1996, elk observed along a 7.4-km transect were counted; identified if they possessed unique characteristics; and classified as calf (young of the year), adult cow, yearling bull, or adult bull. I conducted counts in January because bulls had not cast antlers and visibility in riparian habitats was greater because leaves had fallen. Calves were distinguished from cows by size and all bulls without branched antlers were considered yearlings (Weckerly and Ricca[6] 1995). The southern limit of the transect was 1 km north of Orick, at the junction of Skunk Cabbage Road and State Highway 101. I then proceeded on Highway 101 north to the Gold Bluffs Beach road, which was viewed as far as the Prairie Creek bridge. The transect then resumed along Highway 101 to the Newton P. Drury road and concluded at the northern perimeter of Boyes Prairie. The transect was driven as slowly as possible for 1.5 h in both directions and, if needed, I left my vehicle to obtain unobstructed views of elk spotted from the road. Elk were observed as far as 0.5 km on either side of the road. Elk that were suspected of being tallied more than once were ignored. Between counts, I alternated the starting point from the south to the north terminus.

Population size was computed with the Bowden estimator for two resighting occasions using program NOREMARK (White 1996). The Bowden estimator was computed from the mean and variance of resighting frequencies of individual, unique elk and assumes that unique animals were chosen at random from the population (Bowden and Kufeld 1995). This estimator does not assume homogeneous resighting probabilities among marked animals (White 1996). Homogeneous resightings of individuals are unlikely for elk (Boyce 1989; F.W. Weckerly, pers.

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[5] Weckerly, F.W. 1996. Monitoring populations of Roosevelt elk in dense coniferous forest: Patterns of distribution, development of distribution surveys, and population estimation. California Department of Fish and Game, Sacramento, California, USA.

[6] Weckerly, F.W. and M.A. Ricca. 1995. Developing a reliable population monitoring program of Roosevelt elk occupying dense coniferous forests. California Department of Fish and Game, Sacramento, California, USA.

obs.). Confidence intervals were normalized by obtaining the natural logarithm of population size (Bowden and Kufeld 1995). Density was computed as estimated population size or confidence bounds/area surveyed. Although this approach only crudely measures area surveyed, it does allow direct comparison with previous studies (Houston et al. 1987, Galea[7] 1990).

After estimating population size, I assessed the probable extent of bias in the estimate, its precision (confidence interval length expressed as percent of the estimate), and the coverage of the 95% confidence interval by conducting a Monte Carlo simulation, in NOREMARK, using parameters identical to my results (White 1996). To explore how the reliability of estimates could be improved, I again conducted Monte Carlo simulations and examined bias, precision, and coverage. Parameters that can be controlled to a large extent by the investigator (number of resighting episodes and proportion of the population with unique or marked individuals) were manipulated when the remaining parameters (proportion of population observed and unique individuals seen) were held constant. Two sets of simulations were conducted. One, when the proportion of population observed and unique elk seen was the same as found in this study (0.9 and 0.83) and another set of simulations when these parameters were lower (0.6 and 0.5). All Monte Carlo simulations were replicated 1,000 times using the joint hypergeometric distribution (White 1996).

RESULTS

I identified 15 unique elk: three yearling bulls, six adult cows, and six adult bulls. All bulls were identified from antler anomalies. Three cows were identified from slits in ears, one cow had a tagged ear, and two possessed unusual morphological features. On 24 January, 101 elk were counted: 22 calves, 11 yearling bulls, 52 adult cows, and 16 adult bulls. Twelve unique individuals were sighted. The next morning, 105 elk were observed: 24 calves, 10 yearling bulls, 49 adult cows, and 22 adult bulls. Thirteen unique individuals were observed on that count. For both days combined, the adult bull:adult cow ratio was 0.38:1, the yearling bull:adult cow ratio was 0.21:1, and the calf:adult cow ratio was 0.45:1. The Bowden estimate of abundance was 115 and the 95% confidence interval was 98-134. A more realistic confidence interval was 105-134, because the maximum number of elk observed was 105 (25 January count). Estimated elk density was 16/km^2, with a 95% confidence interval of 14-18. Monte Carlo simulations using a joint hypergeometric distribution suggested that the bias of the population estimate was small (-0.14% or 1.6 animals), confidence interval length was about 24% of estimated abundance, and coverage of the computed 95% confidence interval was 79.5%.

Simulations to assess bias, coverage of the computed confidence interval, and precision were conducted for a population of 115 with 10-30% possessing unique

[7] Galea, F.L. 1990. Mark-recapture for estimation of large animal populations in heterogenous habitats. M.S. Thesis, Humboldt State University, Arcata, California, USA.

features and two, five, or 10 resighting episodes. The projected bias did not vary widely (0 to ± 1.24%) regardless of the proportion of the population observed, proportion of unique elk observed, number of resighting episodes, or proportion of the population with unique elk. Coverage of the 95% confidence interval ranged from as low as 70% to as much as 89% for most combinations of number of resight episodes and proportions of population with unique elk. Lower coverage was found when a smaller proportion of the population contained unique individuals. The precision of estimates did fluctuate more in response to changes in parameters than did bias or coverage (Fig. 1). Confidence interval lengths declined as more of the population contained elk with unique features and more resighting episodes were conducted. When 90% of the population and 83% of unique elk were observed, confidence interval lengths ranged from about 5 to 30% of estimated abundance, whereas, confidence interval lengths increased to about 15 to 70% of the estimate when 60% of the population and 50% of unique individuals were seen. With the exception of two resighting episodes, confidence interval lengths were smaller when 90% of the population and 83% of unique elk were seen, as opposed to counting 60% of the population and 50% of unique elk. On average, for each doubling of the proportion of the population marked (e.g., 0.1 to 0.2) and number of resighting episodes (e.g., 2 to 4), there was, respectively, a 38% and 31% decrease in confidence interval length.

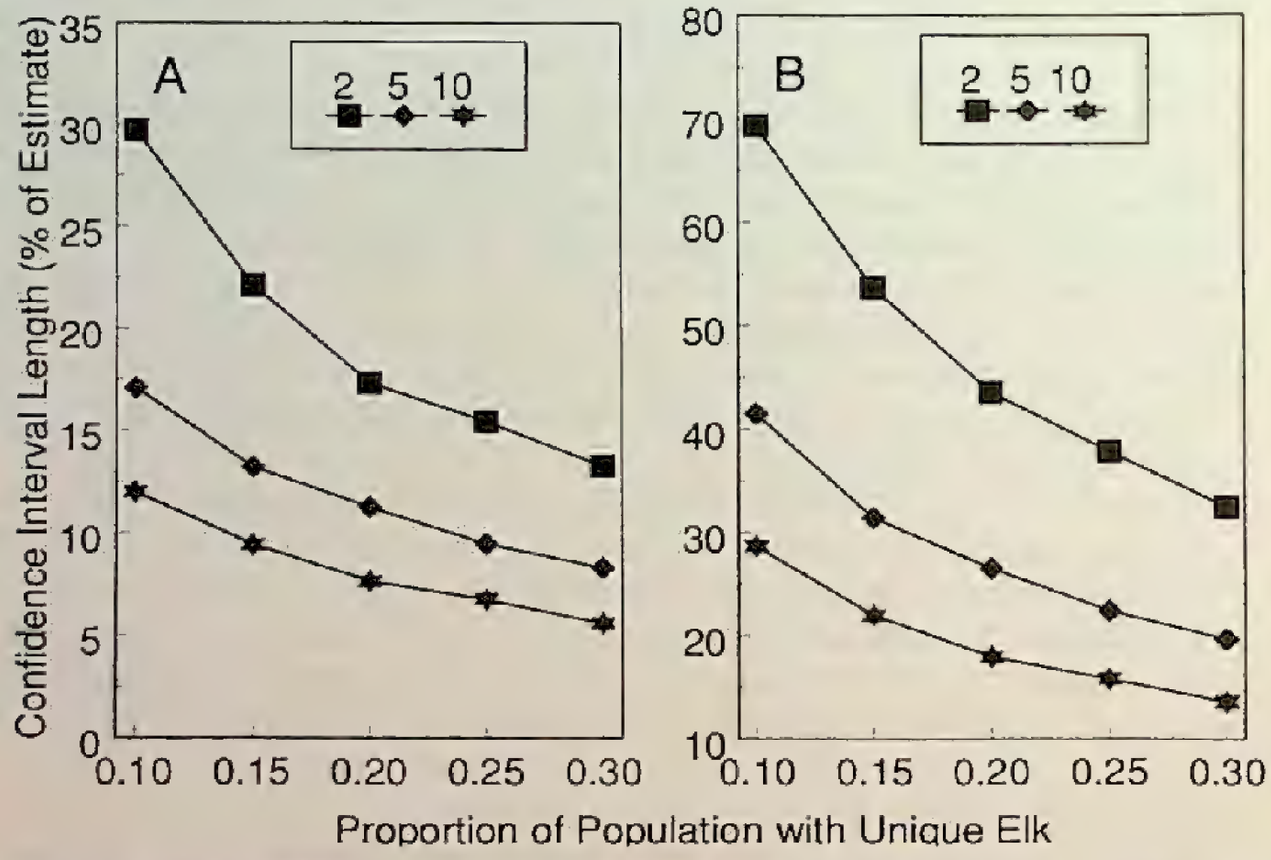

Figure 1. Results of Monte Carlo simulations of 95% confidence interval length of population size estimates when number of resighting episodes (in legend) and proportion of the population with unique elk changes. Sets of simulations were conducted when A) 90% of the population and 83% of the unique individuals were observed and B) when 60% of the population and 50% of unique individuals were seen.

DISCUSSION

This method is a repeatable and apparently reliable way to estimate abundance of an unhunted population that is readily observable from a road. Bias of the estimate appears small and the confidence interval length is less than 40% of the estimated population size, suggesting good precision (White et al.[5] 1982). Furthermore, this method is less costly than other methods typically used to estimate elk populations (Houston et al. 1987, Galea[7] 1990). No expense is required to capture and mark elk or to conduct aerial surveys. Major costs include use of a vehicle, salary for one technician to observe elk and conduct surveys, and a high-powered spotting scope.

Similar to Harper et al. (1967), Franklin[3] (1968), Lieb[4] (1973), and Bowyer (1981), I found no systematic way to identify unique elk. Careful observation of individuals is required and a catalog of photographs of individuals with unique features is useful. Rump patches, dorsal coloration, and ear shape and color were not diagnostic, as noted in another population of elk (Clutton-Brock et al. 1982). Observation of elk should take place in autumn so that bulls with unique antler configurations and dimensions can be included in counts conducted that winter. Because antler dimensions change yearly, unique elk must be identified annually.

Monte Carlo simulations indicate that the most effective way to improve the reliability of population statistics is to increase the number of resighting episodes and observe a high proportion of the population. This can be done without increasing costs substantially if elk remain habituated to humans so a high proportion of the population can be observed.

Because many elk were tallied during counts, it seems possible to assess population trends by conducting surveys and simply computing means and standard errors of the number of elk detected. As it is relatively easy to identify individuals with unique features, mark-resight surveys should be conducted for a minimum of 5 yr, or until a detectable change in population size occurs. This would help determine if the fraction of marked animals observed each year is similar. If so, the proportion of the population observed should be similar among years and switching to an index of abundance may be more cost effective.

My herd composition estimates are difficult to compare with other populations of Roosevelt elk because estimates were obtained in different seasons when sex and age composition may differ due to changes in survival and detectability (McCullough et al. 1994). Nevertheless, a hunted population near Smith River, Del Norte County, California, had calf:cow and bull:cow ratios of approximately 0.30:1 and 0.16:1 in April and May (Weckerly and Ricca[6] 1995). The lower sex ratio than found in my study is probably due to hunting of bulls. In Clatsop, Tillamook, Lincoln, and Curry counties, Oregon, calf:cow and bull:cow ratios ranged from 0.26 - 0.64:1 and 0.02 - 0.50:1 (Graff 1955).

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[5] White, G.C., D.R. Anderson, K.P. Burnham, and D.L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory. LA8787-NERP. Los Alamos, New Mexico, USA.

Comparing my estimated density (16 elk/km^2) with two other studies conducted in areas considered to have abundant elk populations suggests a high density population along Prairie Creek. Using a mark-recapture estimator from aerial surveys, Galea[7] (1990) calculated that 15 elk/km^2 (95% confidence interval = 11-22) inhabited second-growth redwood-conifer and marsh habitat near Big Lagoon, Humboldt County. In old-growth rain forests of the Olympic National Park, Washington, Houston et al. (1987) calculated densities of 11-16 elk/km^2 from aerial surveys. Based on intensive ground searches, Weckerly[5] (1996) reported 2.2 elk/km^2 inhabiting an industrial forest in Del Norte County.

Population data for non-hunted Roosevelt elk herds could be used to formulate plans for translocation programs, to assess elk-vehicle accidents, to document response of the population to unpredictable future disturbances, and to measure impacts of elk herbivory on composition and structure of plant communities. Moreover, a time series from an abundant population would be useful for exploring such fundamental concepts as population equilibrium and carrying capacity.

ACKNOWLEDGMENTS

Funding was provided by Contract Numbers CA94224 and CA95212 from the Elk Management Program, California Department of Fish and Game and the Rocky Mountain Elk Foundation. D. Koch, H. Sakai, and an anonymous reviewer offered useful comments on earlier drafts of the manuscript.

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Received: 25 July 1996
Accepted: 23 September 1996

California Fish and Game 82(4):182-186 1996

PHOTOGRAPHIC EVIDENCE OF WHITE SHARK MOVEMENTS IN CALIFORNIA WATERS

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The white shark, *Carcharodon carcharias*, occurs throughout California waters, but ranges of individuals are unknown. The South Farallon Islands (SFI) are a group of small rocky islands, located approximately 30 km west of San Francisco, California (37°42' N, 123°00' W), where research on white shark ecology, behavior, physiology, and localized movements has been conducted (Ainley et al. 1981, 1985; Klimley et al. 1992, 1996; Anderson et al. 1996 a, b; Goldman[2] 1996; Goldman et al. 1996; Klimley and Anderson 1996; Pyle et al. 1996). Adult white sharks prey on pinnipeds, primarily juvenile northern elephant seals, *Mirounga angustirostris*, during the fall months off SFI (Ainley et al. 1981, 1985).

Although individual white sharks have been resighted at SFI in the same and different years (Klimley and Anderson 1996; Anderson and Goldman, unpubl. data), none have been resighted and identified at other locations. Using photographs of dorsal fins to identify individual white sharks, we present the first alternate location resightings of two white sharks off California and suggest that photo identification is a valid method for identifying individual white sharks over long time periods.

Photo identification methods have been used effectively with whales and dolphins. Photographs of distinctive fins and markings on individuals allow them to be re-identified at a later date (Leatherwood et al. 1990, Hammond et al. 1990). This method has also been effective with white sharks at SFI (Klimley and Anderson 1996). A white shark's first dorsal and caudal fins often break the surface during feeding, enabling the fins to be photographed. The trailing edges of dorsal fins have distinctive arrangements of notches that are unique to each individual. Shape of dorsal fins also varies (rounded vs. pointed). We have observed that the notches and shape remain unchanged for long periods of time (also see Klimley and Anderson 1996). Dorsal and caudal fins of white sharks have been photographed at SFI since

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[1] Current Address: The College of William and Mary, School of Marine Science, Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

[2] Goldman, K.J. 1996. Thermal physiology and behavioral ecology of white sharks, *Carcharodon carcharias*. M.A. Thesis, San Francisco State University, San Francisco, California, USA.

1988 and more than 20 known individuals have been resighted in 2 or more years (Klimley and Anderson 1996; Anderson and Goldman, unpubl. data). Most photographs were taken using 35 mm, ISO 100 slide film.

The first shark presented here was initially photographed from shore at SFI on 7 November 1988 and resighted on 18 October 1994 off Newport Beach, California (33° 28' N, 118° 10' W), > 700 km south of SFI, in water approximately 550 m deep (Fig. 1A and B). The shark was at large for 2,170 d (6.1 yr). The initial sighting was

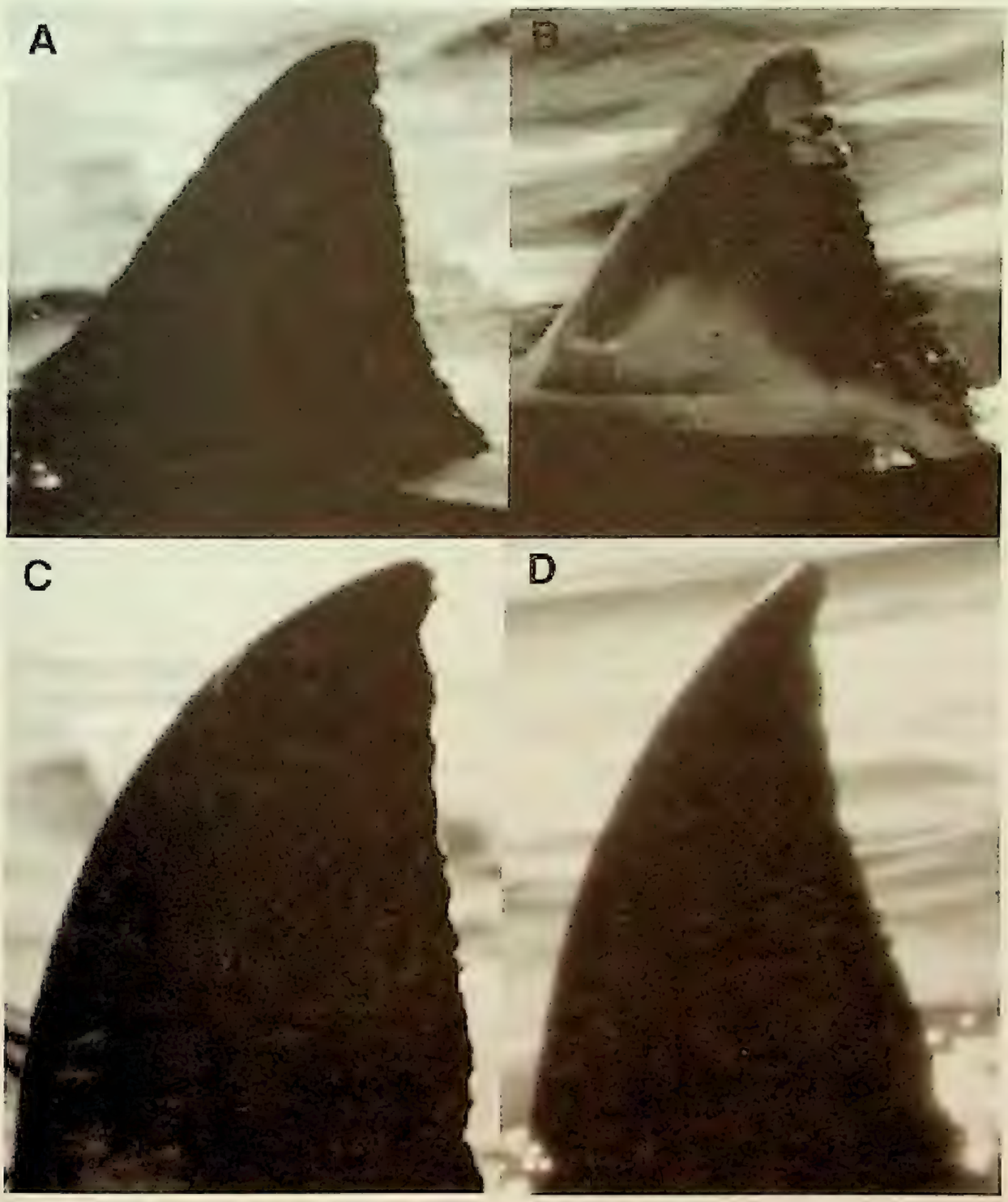

Figure 1. A) Photo of shark #1 from the South Farallon Islands, 7 November 1988; B) Photo of shark #1 from southern California, 18 October 1994; C) Photo of shark #2 from South Farallon Islands, 5 October 1991; D) Photo of shark #2 from Tomales Point, 28 September 1994.

at a seal decoy that was drifting approximately 75 m off the southeast side of SFI to lure a shark to the surface (For a description of the decoy technique, see Anderson et al. 1996a.). After 15 min, a shark attacked the decoy and its dorsal and caudal fins were photographed (Fig. 1A).

The resighting of the first shark occurred in an interesting manner. A spotter plane, working in cooperation with the University of California at Los Angeles research vessel *SEA WORLD* to locate swordfish, came across a large blood stain. The pilot was unsure what he had found, stating "it looked as if someone had dumped red paint into the water." Upon arrival, the *SEA WORLD* discovered a predatory attack in progress; a large white shark was feeding on a 200-300-kg northern elephant seal. C. Gardner, a professional photographer, photographed the feeding shark and put out a local press release (P. Thomas, a writer from the Los Angeles Times, forwarded the photographs to the authors.). We were able to match the photo to the shark from 7 November 1988 (Fig. 1B).

The second shark presented here was initially photographed at SFI from the San Francisco State University research vessel *HAPLOOPS* on 5 October 1991 and resighted on 28 September 1994 following an attack on a harbor seal, *Phoca vitulina*, approximately 200 m northwest of Tomales Point, California (38° 15' N, 123°00' W), > 70 km north of SFI in water approximately 9.5 m deep (Fig. 1C and D). The shark was at large for 1,092 d (3.1 yr). The initial sighting occurred following an attack on a pinniped approximately 50 m off the south side of SFI. A blue seat cushion was presented on the ocean surface to attract the shark and the shark's dorsal and caudal fins were photographed when the shark surfaced to investigate the cushion. At the resighting, the shark was again lured to the surface with a blue seat cushion (by the authors) and photographed in the same manner as it was at SFI in 1991. Two sharks were present at this event and the smaller individual was also photographed, but no match has been found.

These resightings shed some light on how far individual white sharks may range. Obviously, more data are needed to draw conclusions about white shark movements off California. The time necessary for the first shark to travel the relatively long distance is unknown as this animal has not been observed at SFI since its original sighting. However, if this shark is a female, this pattern might fit the hypothesis that large females migrate into southern California waters to pup (Klimley 1985). When and how often white sharks travel long distances off California is unknown. The second shark has also not been seen at SFI since its original sighting. Although 3-6yr passed between sightings, the dorsal fins of these two white sharks remained virtually unchanged (Fig. 1). This suggests that photographic identification of white sharks is reliable over long periods of time. Photographs may be more reliable (particularly for this species) than tagging as tags can be shed and, to identify a shark, the tag must be retrieved either by physically removing it or capturing the shark.

It is interesting that all sightings occurred in the fall and that the original sightings and both resightings involved predation on pinnipeds. Many recognizable white sharks have been sighted over several consecutive seasons at SFI; some have been sighted every other season, and others have been sighted only once (Klimley and

Anderson 1996; Anderson and Goldman, unpubl. data). The two resightings we report may indicate alternate feeding locations for white sharks when they are not seen at SFI in one or more fall seasons.

ACKNOWLEDGMENTS

We thank the Gulf of the Farallones National Marine Sanctuary, the U.S. Fish and Wildlife Service, and the Point Reyes Bird Observatory for access to the SFI. Thanks to San Francisco State University for the use of the R/V *HAPLOOPS*, P. Thomas (Los Angeles Times) and M. Shead (Hubbs Research Institute) for information about the resighting of the first shark, and C. Gardner for the photograph. Special thanks go to S. Maruta and S. Anderson for help in preparing the photographs. Thanks to R. Larson, D. Kohlhorst, J. Orsi, and three anonymous reviewers for their comments on the manuscript and to P. Pyle and D. Huntwork for help in the field.

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Received: 5 September 1996
Accepted: 9 December 1996

CALIFORNIA FISH AND GAME
California Fish and Game 82(4):187-191 1996

PRELIMINARY ESTIMATE OF RICE PRESENT IN STRIP-HARVESTED FIELDS IN THE SACRAMENTO VALLEY, CALIFORNIA

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Rice is critical winter food for the large populations of migratory waterfowl in the Sacramento Valley (Miller 1987, Miller et al. 1989) because remaining wetlands are limited and do not supply all required food resources (Heitmeyer 1989). An average of 388 kg/ha of rice is present in conventionally harvested fields in the Sacramento Valley (Miller et al. 1989). This rice is potentially available for wintering waterfowl and other birds to consume, although 20-25% may not be accessible because of the presence of straw (Clark and Greenwood 1987). An updated assessment of the quantity of rice seed present in harvested fields is needed because a new harvesting technology was introduced to the Sacramento Valley in 1990, potentially changing the amount of rice available to migratory birds. The new method uses a "stripper header" attached to the combine harvester as a replacement for the conventional cutter-bar header (Bennett et al. 1993). This relatively inexpensive (about US$30,000) innovation allows faster harvest (3.2 - 12.8 km/h) than with conventional headers (1.6 km/h).

The conventional cutter-bar header cuts the plant stems, creating stubble, and pulls the seedheads and cut straw into the machine. Threshing components separate and retain the seeds and the straw is carried out the back to fall on the ground. Loose seeds and seeds still attached to incompletely processed seedheads become waste rice. Additional waste rice results from shatter as the machine passes through the field and impacts adjacent rice plants.

In contrast, the stripper header consists of a rotor with hundreds of stripping teeth attached. The rotor revolves at about 500 rpm, strips the seeds from the seedheads, and sweeps them into the harvester for storage. Thus, the machine does not process cut straw. Some seeds are lost out the back of the machine and shatter still occurs, but few seeds are retained by seedheads after stripping and the potential for wasted grain is reduced. Use of stripper headers will likely increase over time, because they allow faster harvest. This note provides estimates of their efficiency to better predict potential riceland food supplies for wintering waterfowl.

In fall 1985, the U.S. Fish and Wildlife Service sampled 111 conventionally cut rice fields at a rate of two plots per field (Miller et al. 1989). In 1986, investigators sampled 15 fields using eight plots per field. In fall 1993, we repeated methodology from 1986 and sampled eight plots in each of 17 stripped fields. The use of strippers was limited in 1993. Therefore, rather than use a strictly random selection process

to obtain sample fields, which would have been inefficient, we located a sufficient number of growers who were going to use strippers in 1993 by consulting a list supplied by University of California farm advisors and from our own phone query of growers that participated in the 1985-86 studies (Miller et al. 1989). From the growers known to be using strippers, we obtained the location and total number of fields that would be stripped. From these, we randomly selected sample fields in Butte (n = 3), Colusa (n = 4), Glenn (n = 2), Sutter (n = 3), Yuba (n = 3), Yolo (n = 1), and Sacramento (n = 1) counties, a similar county distribution as in 1986 (Miller et al. 1989). All stripper headers were of identical make (Shelbourne-Reynolds Engineering, Suffolk, England), but they were mounted on a variety of combine harvesters. Each of the 17 sampled fields was harvested with a different stripper header by a different harvester operator.

In 1993, we repeated field sampling procedures used in 1985-86 (Miller et al. 1989). We used 0.3 m x 5.5 m plots randomly located within fields perpendicular to direction of harvester travel. We collected samples with wet/dry vacuums powered by portable generators and then threshed, cleaned, hand separated, dried, and weighed (dry weight) the seeds.

We used pooled 1985-86 data (Miller et al. 1989) to estimate overall average weight of rice present (kg/ha) in the Sacramento Valley. However, we used only 1986 data to compare with 1993 field averages, because the two plots sampled in each field in 1985 would not produce reliable estimates by field. In 1985, Miller et al. (1989) obtained estimates of rice remaining on the ground and in the cut straw (laying on the stubble) in each of 22 plots (11 fields). We multiplied this resulting percentage by the pooled estimate for total rice present in 1985-86 to obtain estimates of weight of rice in the straw and on the ground. In 1993, we obtained separate straw (rice retained on seedheads after stripping) and ground estimates for all plots.

Budget constraints in 1993 precluded sampling conventionally harvested fields as controls. Instead, we compared 1993 strip-harvest results with pooled 1985-86 data (Miller et al. 1989). In addition, the U.S. Department of Agriculture (USDA) obtained additional estimates from 1985 to 1989 (USDA[1] 1985), and those obtained in 1985-86 were very similar or identical to the results of Miller et al. (1989) for those years. Thus, we concluded that the USDA data reliably measuredconventional-harvest loss through 1989, when the program was terminated. In addition, contacts with agricultural interests and rice growers convinced us that no important changes to conventional harvest had been made since 1989 that would have measurably altered harvest loss. Thus, we elected to use 1985-89 values to broadly represent rice in conventionally harvested fields for comparison with stripper results in 1993, but cautious interpretation of results is advised. We used *t*-tests to compare strip- and conventional-harvest results and chi-square analyses to compare sample distributions in stripped and conventionally harvested plots and fields.

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[1] U.S. Department of Agriculture (USDA). 1985. Enumerator's Manual, 1985 Rice Objective Yield Survey. Crop Reporting Board, Statistical Reporting Service, USDA, Washington, D.C.

The mean amount of rice left after strip harvest in 1993 (344 kg/ha) was not statistically different ($t = 1.42$, $df = 475$, $P > 0.05$) from the pooled mean of 388 kg/ha for conventionally harvested fields in 1985-86 (Table 1). The point estimate of rice available to waterfowl in strip-harvested fields in 1993 was less than all USDA estimates for conventional harvest through 1989 (375, 395, 368, 627, and 468 kg/ha for 1985 through 1989) (G.K.H. Chong, California Agricultural Statistics Service, Sacramento, California, pers. comm.). Rice available in conventionally harvested fields may have been higher still in 1993 because harvest losses correlate positively with yield (Miller et al. 1989) and average yield was 9,320 kg/ha in 1993 compared to 7,885-8,750 kg/ha from 1985 to 1989 (California Agricultural Statistics Service, Sacramento, California).

An average of about 290 kg/ha of rice was left on the ground with both harvest techniques (Table 1). However, strip harvest left significantly less seed in the straw (52 kg/ha or 15% of total) than did conventional harvest (97 kg/ha or 25% of total) ($t = 2.18$, $df = 155$, $P < 0.05$) (Table 1). Thus, strip harvest in 1993 left about 45 kg/ha less rice in fields than did conventional harvest in 1985-86.

The majority of sample plots contained an equivalent of ≤ 500 kg/ha of rice with both harvest techniques (Fig. 1); however, rice was more uniformly distributed in conventionally cut fields than in strip-harvested fields ($\chi^2 = 19.56$, $df = 8$, $P < 0.05$). For example, in conventional fields, only 36% of individual sample plots had ≤ 250 kg/ha of rice, but in stripped fields, 51% of plots contained ≤ 250 kg/ha (Fig. 1). Similarly, when comparing field means (Fig. 2), only 27% of conventional fields averaged ≤ 250 kg/ha compared with 42% of stripped fields; however, the frequency distributions were not significantly different ($\chi^2 = 1.17$, $df = 6$, $P > 0.05$), possibly because the number of fields sampled was small.

In 1993, harvester operators were still learning the most efficient way to use strip-harvest technology. We saw evidence of poor stripper control in many fields, such as excessive amounts of rice on the ground in some areas and unharvested patches in other areas of the same fields (see Fig. 1). Much of this variability probably

Table 1. Mean weight (and standard error) of rice (kg/ha) in conventionally harvested (1985-86 pooled; Miller et al. 1989) and strip-harvested (1993) rice fields in the Sacramento Valley, California.

	Ground	Straw	Percent in straw[a]	Total	No. of Plots
Conventional	291(37)[b]	97 (17)[b]	25	388(20)	341
Stripped	292(37)	52 (6)	15	344(28)	136

[a] Percentage of rice in straw for conventional harvest was obtained in 1985 using straw/ground comparisons in 22 plots (see text), and this percentage was applied to Total to derive the Ground and Straw results shown for conventional harvest. Straw data for Stripped were obtained in all plots in 1993.

[b] S.E.s for Ground and Straw for conventional harvest are S.E.s from the straw/ground data obtained from 22 plots in 1985 (see text) because estimates could not be obtained for pooled 1985-86 data except for Total.

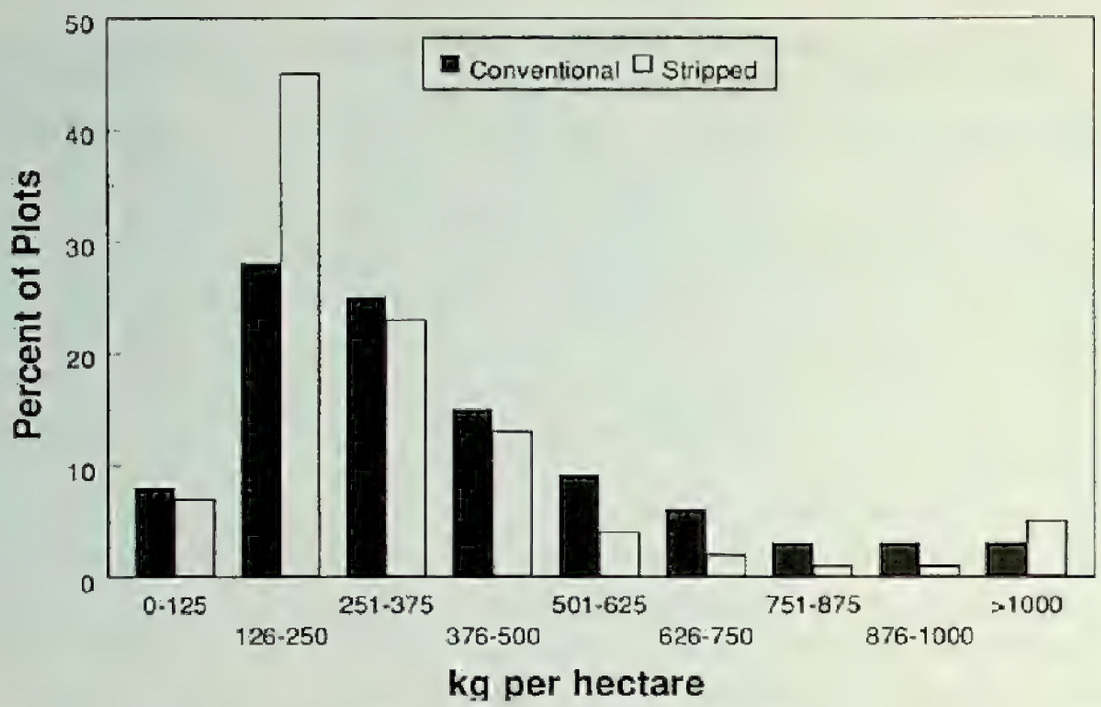

Figure 1. Proportionate distribution of rice remaining after harvest among sample plots in conventionally harvested (1985-86 pooled; Miller et al. 1989) and strip-harvested (1993) rice fields in the Sacramento Valley, California.

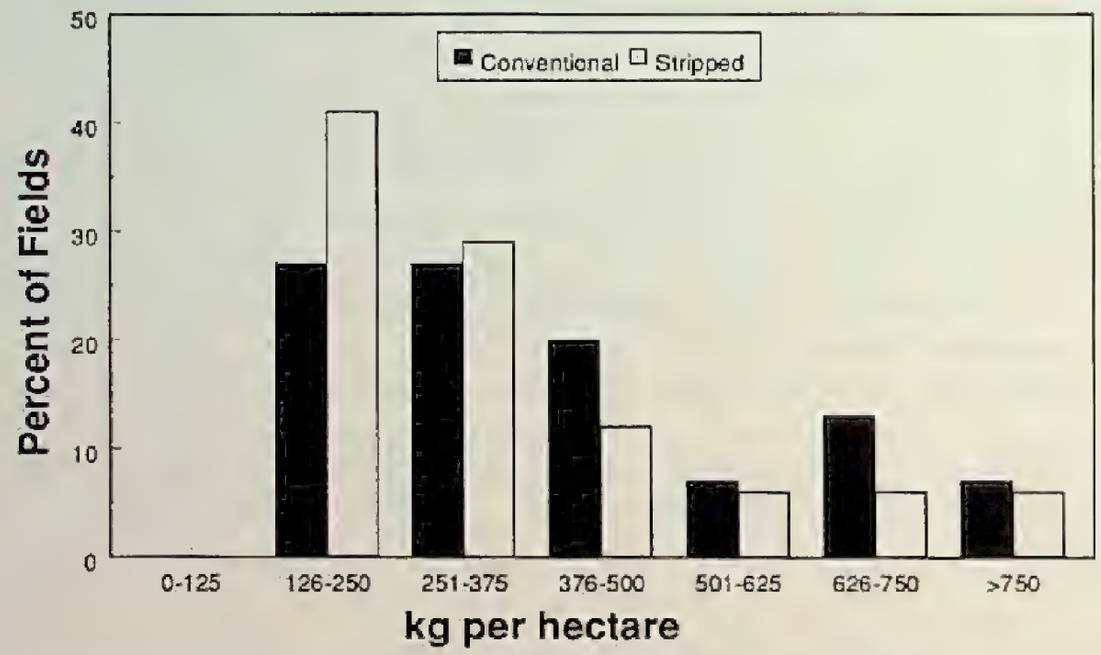

Figure 2. Proportionate distribution of rice remaining after harvest among fields in conventionally harvested (1986; Miller et al. 1989) and strip-harvested (1993) rice fields in the Sacramento Valley, California.

resulted from excessive harvester speed (Bennett et al. 1993). As practical knowledge of stripper use improves, harvest efficiency may increase. Given the speed and low cost of strippers, we expect their use to expand markedly and our results should be verified with additional investigation when the operational use of this technology matures in the years ahead.

Our results show that the total amount of rice present in stripped fields in 1993 was not markedly different from that in conventionally harvested fields in previous years and the difference we found resulted solely from the reduced amount of seed retained in the straw. Given the large quantity of rice remaining in strip-harvested fields, food supply for wintering waterfowl may still be adequate. However, the relative foraging efficiency of waterfowl in strip-harvested and conventionally cut fields is not known, although the tall (usually >1 m) straw left standing after stripping has been shown to deter use by foraging geese (J. Day, U.S. Geological Survey, Biological Resources Division, Dixon, California, unpubl. data). Mowing may be needed to accommodate foraging waterfowl. Also, the probability of waterfowl locating productive foraging areas will be reduced in regions dominated by stripper harvest because the distribution of seed in stripped fields is less uniform than in conventionally harvested fields.

Our results have implications for waste rice availability to waterfowl in Arkansas, Texas, Louisiana, and other rice growing regions in waterfowl wintering range, because stripper use is increasing there as well. Also, stripper headers are used to harvest wheat and barley and this technology is now being widely used in the Klamath Basin. Efficiency of stripper technology needs to be assessed for other regions and crops to determine if waterfowl foraging opportunities may be impacted.

ACKNOWLEDGMENTS

We thank the 17 Sacramento Valley rice growers who granted us permission to collect samples on their land. University of California Farm Advisors S. Scardaci and J. Williams provided names of growers who would be using stripper headers in 1993. J. Day, M. Casazza, J. Fries, and D. Storm assisted in collecting and processing rice samples.

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Received: 5 September 1995
Accepted: 13 October 1996

California Fish and Game 82(4):192-194 1996

A PACIFIC FAT SLEEPER, *DORMITATOR LATIFRONS* (PERCIFORMES:ELEOTRIDIDAE), FROM LAKE MERRITT, SAN FRANCISCO BAY, CALIFORNIA

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The Pacific fat sleeper, *Dormitator latifrons* (Richardson 1844), lives in coastal marine, brackish, and fresh waters of the eastern Pacific Ocean from Ecuador to Mexico (Follett 1961, Allen and Robertson 1994, Watson 1996); a single specimen is known from coastal marine waters of southern California (Fitch 1962). This specimen, 230 mm standard length (SL), was caught by hook and line off a rocky shoreline near Palos Verdes, Los Angeles County (33°47'N, 118°26'W) on 8 July 1961. It is now in the Marine Vertebrates Collection at the Scripps Institution of Oceanography (SIO 61-401). Recently, a second California specimen was collected from Lake Merritt within the San Francisco Bay complex, representing the most northern locality known for the species and a range extension of >600 km. Although this is a new locality record for the species, the possible origin of the specimen in Lake Merritt can only be surmised.

The specimen was found by R. Bailey of the Lake Merritt Institute during a routine survey of Lake Merritt in Oakland, Alameda County, California (37°47.60'N, 122°15.10'W). Lake Merritt is a brackish estuary that takes freshwater runoff from the surrounding Oakland and Piedmont hills and adjacent metropolitan area and is connected to San Francisco Bay via a canal to the Port of Oakland in Oakland Harbor on the east side of the bay. The *D. latifrons* was collected from shallow water (about 1 m) in Lake Merritt, west of the boating center docks at Lakeside Park at approximately 1000 on 7 October 1995. It was frozen soon thereafter, but subsequent defrosting and refreezing caused minor damage to the fish. The specimen was donated to the Department of Ichthyology, California Academy of Sciences, where it was preserved and catalogued (CAS 87870).

Identification as *D. latifrons* was based primarily on the large size of the individual (212.5 mm SL), separate ventral fins, heavily scaled body, large and wide dorsally depressed head, and relatively small upturned jaw that did not extend posteriorly beyond the small eyes. The specimen was grayish-blue overall. It had thin dark bars on the soft dorsal and anal fins, as well as a dark postopercular spot on each side of the body and a dark vertical bar at the base of the pectoral fins. Fin ray counts were D VII+I, 9; Pectoral 1+14; Pelvic I, 5; A I, 9; all in agreement with meristic counts given in Miller and Lea (1972) and Allen and Robertson (1994). Additionally, comparison with other *D. latifrons* specimens from Latin America in the CAS collection confirmed the initial identification.

The mode of introduction of this specimen into the San Francisco Bay area is subject to speculation. Larvae believed to be from *D. latifrons* have been collected from marine waters off western Mexico (Watson 1996). Possibly, the Lake Merritt specimen was carried north from southern California or Mexico in its larval form by the warm 1983 or 1991 El Nino currents and later settled in San Francisco Bay. This natural transport mechanism has been used to explain the extralimital occurrences of some Mexican species in southern California waters (Fitch 1962, Lea et al. 1989, Moore 1991, Lea and Rosenblatt 1992). It is also possible that this specimen was released alive into the lake (Lachner et al. 1970), but this is unlikely since the species is rarely sold as an aquarium fish in California and is not sold in the live fish markets in the area.

The most plausible explanation is that the specimen arrived in egg, larval, or juvenile form in ballast water discharged into Oakland Harbor from a cargo ship coming from Latin America (Carlton 1985); the fish could have traveled to Lake Merritt from there. This is also the suspected transport mechanism for the eleotridid, *Prionobutis koilomatodon*, from Indo-west Pacific waters to Panama, where it is now established (Dawson 1973). Additionally, at least three species of Asian gobies (yellowfin goby, *Acanthogobius flavimanus;* chameleon goby, *Tridentiger trigonocephalus;* and shimofuri goby, *T. bifasciatus*) may have arrived in California by this means and are now established in marine, brackish, and freshwaters of San Francisco Bay and other areas of California (Brittan et al. 1963, Haaker 1979, Matern and Fleming 1995). Both *A. flavimanus* and *T. trigonocephalus* have been collected from Lake Merritt. If ballast water transport is the method of introduction for *D. latifrons*, it is possible that additional specimens are living in San Francisco Bay and that more may be caught in the future.

ACKNOWLEDGMENTS

I thank R. Bailey of the Lake Merritt Institute for bringing the specimen to my attention, for donating it to the California Academy of Sciences, and for information on the ichthyofauna of the lake. Thanks also to J. McCosker, C. Ferraris, and J.D. Fong of the Department of Ichthyology, California Academy of Sciences and H.J. Walker Jr. of Scripps Institution of Oceanography for assistance.

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Received: 3 June 1996
Accepted: 12 December 1996

California Fish and Game 82(4):195-196 1996

THE RAGGED-TOOTH SHARK, *ODONTASPIS FEROX* (RISSO, 1810), IN THE GULF OF CALIFORNIA.

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The ragged-tooth shark, *Odontaspis ferox* (Risso, 1810), is an uncommon and poorly known species found typically on, or associated with, the bottom in deep water along continental and insular shelves and upper slopes (Compagno 1984). The maximum total length (TL) is 367 cm (323 kg eviscerated weight) (Seigel and Compagno 1986). Most aspects of its reproductive biology are unknown (Compagno 1984). Bonfil (1995) summarized the known worldwide records of *O. ferox* and found that it has a cosmopolitan, but disjunct, distribution. In the eastern North Pacific Ocean only five specimens have been recorded, all from Southern California: two by Daugherty (1964) and three by Seigel and Compagno (1986). The species has been noted from Islas San Benito off Central Baja California, Mexico (R.N. Lea, California Department of Fish and Game, pers. comm.). Previously, Kato et al. (1967) stated that it may inhabit the Gulf of California and Galvan et al. (1989) maintained that it is "rare" in the region. However, this paper describes the first confirmed records of the ragged-tooth shark in the Gulf of California.

The first specimen was taken on 21 May 1994, during the shark fishing season in the Midriff Islands of the Gulf of California, when a female ragged-tooth shark (364 cm TL, 284 cm precaudal length, and 330 kg whole weight) was caught at night in a drift gill net near Tiburon Island (28°30'N, 112°33'W). Identification as *O. ferox* was based on teeth, with two or three lateral cuspids arranged characteristically in the jaws (Daugherty 1964, Compagno 1984). The dental formula of the specimen is 24-23/20-19. The jaws are deposited in the Museo de Historia Natural de la Universidad Autonoma de Baja California Sur (MHN-UABCS No. 1883). The dead specimen was dull red. The oviducts were empty, without eggs or embryos, and only the right ovary was functional and enlarged; it contained hundreds of ova (modal diameter = 3 mm). These characters are similar to those of another intrauterine cannibalistic species, the sand tiger shark, *Odontaspis taurus* (Gilmore et al. 1983).

On 1 May 1995, a second jaw of a ragged-tooth shark was collected from fishermen in Isla Cerralvo, southern Gulf of California (MHN-UABCS, uncatalogued). Its dental formula is 28-28/23-23.

These specimens confirm the presence of the ragged-tooth shark in the Gulf of California, where it may be an infrequent bycatch species in the shark fishery.

ACKNOWLEDGMENTS

I am grateful to H. Bonilla and R. Lea for help and comments and to V. Lucero and G. Estrada for field assistance. Financing was provided by the Universidad

Autonoma de Baja California Sur, Grant PII-93-01-CM.

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Received: 3 May 1996
Accepted: 16 September 1996

California Fish and Game 82(4):197-198 1996

BOOK REVIEW

BRUSHFIRES IN CALIFORNIA: ECOLOGY AND RESOURCE MANAGEMENT. Edited by J.E. Keeley and T. Scott. 1995. International Association of Wildland Fire, Fairfield, Washington, USA. ix + 220 pages. $30.00, paper. This is the proceedings of a Southern California Academy of Sciences symposium held 6-7 May 1994 at the University of California, Irvine. The symposium was prompted by heightened awareness of, and renewed debate over, wildland fire and vegetation management following the multitude of firestorms that struck southern California in late October and early November 1993. This collection of 33 papers represents 52 authors and includes (i) perspectives on the important and contentious issues of wildfire and fuel management, (ii) original research on the effects of fire and results of post-fire monitoring and management efforts, and (iii) conservation and management overviews. We discuss selected papers from each of the proceedings' three sections.

SECTION I. Prefire Landscapes Along The Wildland Urban Interface addresses management and conservation issues of wildland fire at a habitat and ecosystem level. T. Scott's introductory overview focuses on spatial patterns between urban development and remaining wildlands, emphasizing effects of habitat fragmentation and pre-fire management challenges. R. Minnich discusses fire regimes in southern California chaparral and postulates the role of time intervals. W. Tippets et al. discuss effects of the 1993 fires on California's coastal sage scrub community and examine the importance of fire management planning in the design of reserves.

SECTION II. Fire Impacts on Animal Populations assesses effects of wildfire and prescribed fire on small mammals and birds in some southern California ecosystems. M. Price et al. report on the effects of controlled burning in habitat of Stephens' kangaroo rat, *Dipodomys stephensi*, at Lake Perris State Recreation Area and the response of other native rodent species to a 1979 arson fire at the University of California's Motte Rimrock Reserve. W. Wirtz reports on responses of several native rodent species to wildland fire and prescribed fires of differing intensities at the USDA Forest Service's San Dimas Experimental Forest. D. Bontrager et al. describe the effects of the 1993 Laguna Canyon fire on populations of California gnatcatcher, *Polioptila californica californica*, and cactus wren, *Campylorhynchus brunneicapillus*.

SECTION III. Postfire Recovery and Management presents post-fire habitat and species recovery, watershed rehabilitation, and management considerations. J. Keeley et al. provide an overview of management issues raised by the southern California wildfires of 1993 and evaluate 1st-year results of monitoring studies from the Old Topanga, Laguna Canyon, and Kinneloa fires. J. Beyers et al. report on 1st-year results of a post-fire seeding experiment conducted on wildlands at the San Diego Wild Animal Park. S. Conard et al. discuss existing knowledge of the impacts of post-fire grass seeding on chaparral ecosystems, including negative impacts to the cover and composition of native herbaceous vegetation, and identify key issues for future studies. J. O'Leary examines potential impacts from post-fire artificial seeding

efforts on cover and diversity patterns in chaparral and coastal sage scrub communities. T. Keeler-Wolf reviews post-fire emergency seeding practices and implications in a conservation context, arguing for reduced reliance upon artificial seeding and, instead, a focused approach to post-fire rehabilitation and erosion control. P. Zedler looks at biological effects of fire frequency in southern California's shrublands and discusses management options. The California Department of Forestry and Fire Protection and USDA Forest Service and Soil Conservation Service present the agencies' rationale and policies for emergency post-fire rehabilitation, including guidelines and recommendations for aerial seeding. D. Magney and E. Roberson offer a thorough, concise, and well-referenced position paper arguing the California Native Plant Society's opposition to artificial seeding following wildfires. T. St. John provides a thought-provoking essay, "A Scientific Basis for Abandonment of Ryegrass Seeding."

We highly recommend *Brushfires in California* to those interested in, or responsible for, wildland conservation and management. Though the proceedings contain a few papers that would have benefited from more detailed editorial review, overall the research, information, and discussions should prove extremely valuable for land managers and scientists concerned with fire management issues. Drs. Keeley and Scott are to be commended, not only for their editing, but for organizing the symposium itself, and publishing the proceedings in a timely fashion.

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Editor, ***CALIFORNIA FISH AND GAME***
California Department of Fish and Game
4001 North Wilson Way
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